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CHEMICAL COMPOSITION OF THE SHOOT LEAVES OF THE APPLE LAXTON'S SUPERB, AS AFFECTED BY BIENNIAL BEARING

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THE use of leaf analysis as a means of assessing the nutrient needs of apple trees has received considerable attention from workers in several countries. Results reported by Cain and Boynton (3), Thomas, Mack and Fagan (6) and others, have shown that the amount of fruit carried by the trees is one of the principal factors affecting the composition of the foliage. Apart from the work of Mason (5), however, little information appears to be available relating to the extreme condition, i.e. the case of the truly biennial varieties of apple.

The data presented in this paper were obtained from the analyses of leaf samples taken from a commercial orchard of Laxton's Superb apple trees planted in 1940 on a well-drained medium loam of mixed sandstone-limestone origin, in County Kilkenny, Ireland. This soil is satisfactory for apple culture and the trees have grown well, yielding good crops of high quality fruit. The orchard is in grass, scythed three or four times during the season.

In one part of the orchard the trees received 3 lb. sulphate of ammonia per tree in the early spring of each year, beginning in 1954, while in an adjacent part they received no nitrogen. Adequate manuring with potash and phosphate was practised, a check being kept on the nutrient status of the soil by periodic soil analyses.

In each part six trees were selected, three bearing a crop in 1954 and three not bearing. In subsequent seasons these trees alternated with each other in bearing and not bearing. This biennial habit was due to natural causes, the trees bearing no fruit in their " off " years.

Mid-shoot leaves were gathered from these trees in late summer (Sept.-Oct.) each year for analysis. The leaf samples were dried, ground, and mixed in the usual manner. Nitrogen estimation was carried out by a modified Kjeldahl procedure, calcium and potassium by flame-photometric techniques. Phosphorus was estimated by a modification of the method of the Association of Official Agricultural Chemists (2) and magnesium by a modification of the method of Andersson (1).

Though the work was carried out under conditions of commercial culture, without the advantages of an orchard designed for experimental work, it is considered that the results are of sufficient value to place on record as illustrating some of the factors influencing the foliage composition of Laxton's Superb apple.

EXPERIMENTAL RESULTS.

The chemical composition of the shoot leaves, expressed as a percentage of dry matter, is given in Tables I to IV.

In the initial year, 1954, the effects attributable to the nitrogenous fertilizer, to the crop and to both these in combination are distinguishable. The effects of the nitrogenous fertilizer alone may be seen in the results from the non-cropping trees, where the dressing of sulphate of ammonia led to an increase in leaf nitrogen. This was accompanied by a decrease in phosphorus in the foliage, slight but non-significant decreases in potassium and total bases (Ca+K+Mg) and a slight tendency to an increase in magnesium (Table I).

TABLE I.

Composition of shoot leaves (% dry matter), sampled on 7th and 8th September; season 1954.

Tree No.	Treatment	Yield (bushels)	Ca	P	K	Mg	N	Ca+K+Mg
13	No N	Nil	0·75	0·38	3·2	0·22	1·57	4·17
14	,,	,,	0·77	0·32	2·8	0·22	1·94	3·79
15	,,	,,	0·88	0·30	2·5	0·17	1·57	3·55
			Means 0·80	*0·33*	*2·8*	*0·20*	*1·69*	*3·84*
16	,,	5¼	1·45	0·23	1·5	0·24	1·89	3·19
17	,,	7¼	1·85	0·23	1·5	0·26	2·08	3·61
18	,,	3¼	1·96	0·24	1·1	0·22	1·98	3·28
			Means 1·75	*0·23*	*1·4*	*0·24*	*1·98*	*3·36*
25	Sulphate of ammonia	Nil	0·79	0·25	2·7	0·21	1·94	3·70
26	,,	,,	0·91	0·27	2·4	0·22	2·08	3·53
27	,,	,,	1·03	0·28	2·1	0·20	2·06	3·33
			Means 0·91	*0·27*	*2·4*	*0·21*	*2·03*	*3·52*
28	,,	3½	1·80	0·20	0·8	0·28	2·30	2·88
29	,,	2¾	1·87	0·20	1·2	0·31	2·46	3·38
30	,,	4½	1·50	0·22	1·3	0·24	2·30	3·04
			Means 1·72	*0·21*	*1·1*	*0·28*	*2·35*	*3·10*
Sig. differences (P=0·05)			0·34	0·04	0·55	0·05	0·25	0·52

The trees which received no nitrogen in 1954 show clearly the effects of the crop on the composition of the foliage. The proportions of calcium, magnesium and nitrogen have all increased, though the increase in magnesium just fails to be significant. Phosphorus and potassium have decreased, and there is also a tendency to a decrease in total bases.

Trees 28, 29, 30 demonstrate the effects of nitrogen and crop in combination. While the calcium level is not increased further, the increase in nitrogen is intensified and the increase in magnesium becomes statistically significant. The decreases in phosphorus and potassium have been accentuated.

In Tables II–IV the foliage analysis figures show only a slight tendency to increased nitrogen in the trees receiving three pounds of sulphate of ammonia. Samples taken earlier in the season might have shown a more pronounced effect, since the nitrogen content of apple leaves has been shown to decrease with season (3).

TABLE II.

Composition of shoot leaves (% dry matter), sampled 26th September ; season 1955.

Tree No.	Treatment	Yield (bushels)	Ca	P	K	Mg	N	Ca+K+Mg
13	No. N	14¼	1·42	0·24	1·45	0·24	2·26	3·11
14	,,	10½	1·25	0·29	1·50	0·22	2·30	2·97
15	,,	13¾	1·30	0·24	1·75	0·21	1·86	3·26
			Means 1·32	*0·26*	*1·57*	*0·22*	*2·14*	*3·11*
16	,,	Nil	1·12	0·24	2·23	0·21	2·00	3·56
17	,,	,,	0·71	0·28	2·50	0·18	1·74	3·39
18	,,	,,	0·95	0·37	2·89	0·22	1·46	4·06
			Means 0·93	*0·30*	*2·54*	*0·20*	*1·73*	*3·67*
25	Sulphate of ammonia	10	1·29	0·19	1·25	0·22	2·27	2·76
26	,,	12½	1·60	0·20	1·28	0·22	2·21	3·10
27	,,	6½	1·28	0·18	1·30	0·17	2·08	2·75
			Means 1·39	*0·19*	*1·28*	*0·20*	*2·19*	*2·87*
29	,,	Nil	0·78	0·15	2·45	0·21	1·94	3·44
30	,,	,,	0·97	0·20	2·18	0·22	2·09	3·37
			Means 0·88	*0·17*	*2·31*	*0·21*	*2·01*	*3·40*
Sig. differences (P=0·05)			0·29	0·07	0·30	0·12	0·38	0·40

TABLE III.

Composition of shoot leaves (% dry matter), sampled 6th October ; season 1956.

Tree No.	Treatment	Yield (bushels)	Ca	P	K	Mg	N	Ca+K+Mg
13	No N	Nil	0·64	0·50	2·30	0·19	1·54	3·13
14	,,	,,	0·65	0·58	2·25	0·20	1·55	3·10
15	,,	,,	0·80	0·42	2·85	0·14	1·26	3·79
			Means 0·70	*0·50*	*2·47*	*0·18*	*1·45*	*3·34*
16	,,	7½	1·85	0·26	1·15	0·23	2·22	3·23
17	,,	9	1·75	0·20	1·15	0·19	2·13	3·09
18	,,	7½	1·69	0·18	0·85	0·18	1·87	2·72
			Means 1·76	*0·21*	*1·05*	*0·20*	*2·07*	*3·01*
25	Sulphate of ammonia	Nil	0·95	0·27	2·30	0·18	1·63	3·45
26	,,	,,	0·60	0·28	2·50	0·18	1·50	3·28
27	,,	,,	0·70	0·40	3·40	0·16	1·41	4·46
			Means 0·75	*0·32*	*2·73*	*0·17*	*1·51*	*3·73*
29	,,	3½	1·80	0·17	1·1	0·22	2·08	3·12
30	,,	6½	1·60	0·17	0·95	0·21	1·97	2·76
30A	,,	8	1·70	0·18	1·3	0·18	2·06	3·21
			Means 1·70	*0·17*	*1·12*	*0·20*	*2·04*	*3·03*
Sig. differences (P=0·05)			0·23	0·11	0·68	0·05	0·26	0·78

TABLE IV.

Composition of shoot leaves (% dry matter), sampled 26th September; season 1957.

Tree No.	Treatment	Yield (bushels)	Ca	P	K	Mg	N	Ca+K+Mg
13	No N	10¾	1·3	0·21	1·8	0·23	2·03	3·33
14	,,	9½	1·5	0·22	1·7	0·23	2·37	3·43
15	,,	11	1·5	0·18	1·7	0·22	2·51	3·42
			Means 1·43	*0·20*	*1·7*	*0·23*	*2·30*	*3·39*
16	,,	Nil	0·90	0·28	2·5	0·19	2·14	3·59
17	,,	,,	0·95	0·30	2·6	0·19	1·74	3·74
18	,,	,,	—	—	—	—	—	—
			Means 0·92	*0·29*	*2·5*	*0·19*	*1·94*	*3·66*
25	Sulphate of ammonia	7	1·50	0 19	1·3	0·26	2·62	3·06
26	,,	10	1·60	0·19	1·3	0·27	2·34	3·17
27	,,	6¼	1·80	0·23	1·8	0·24	2·70	3·84
			Means 1·63	*0·20*	*1·5*	*0·26*	*2·55*	*3·36*
29	,,	Nil	1·00	0·29	2·5	0·22	2·46	3·72
30	,,	,,	1·10	0·22	2·2	0·19	1·79	3·49
30A	,,	,,	1·70	0·18	1·9	0·19	1·81	3·79
			Means 1·27	*0·23*	*2·2*	*0·20*	*2·02*	*3·67*
Sig. differences (P=0·05)			0·44	0·07	0·40	0·02	0·50	0·47

Each year, however, the effects of the crop are very marked. The bearing trees show higher levels of foliage nitrogen and calcium, with a tendency for magnesium to increase also. Decreases occur in potassium and in phosphorus, though they are not invariably significant in the latter.

It is evident that, corresponding to the biennial cropping habit of these trees, there is a biennial fluctuation in the nutrient status of the shoot leaf. This is illustrated in Fig. 1 for the trees 13, 14, 15 and 16, 17, 18.

DISCUSSION.

In U.S.A., Cain and Boynton reported on the effects of fruit crop on the composition of the shoot leaves of McIntosh apple trees (3). They compared the results of sampling trees in two successive seasons, there being no fruit in the second season owing to the destruction of the flowers by frost. As they point out, the results therefore " may not represent a true picture of the effect of fruit crop on the mineral content of the foliage, especially with reference to alternate-bearing trees ".

The results reported in the present paper, from truly biennial trees, are in accordance with those of Cain and Boynton. The effect of a crop is to reduce the proportions of potassium and phosphorus in the shoot leaf and to increase those of calcium and nitrogen. The tendency of magnesium to increase also, even though not statistically significant in most years, is in accordance with their findings. It agrees, too, with the observation that, in many orchards in Ireland, bearing trees of Laxton's Superb are much less prone to show foliage symptoms of magnesium deficiency than trees carrying no crop. In the year 1955, for example, this was very

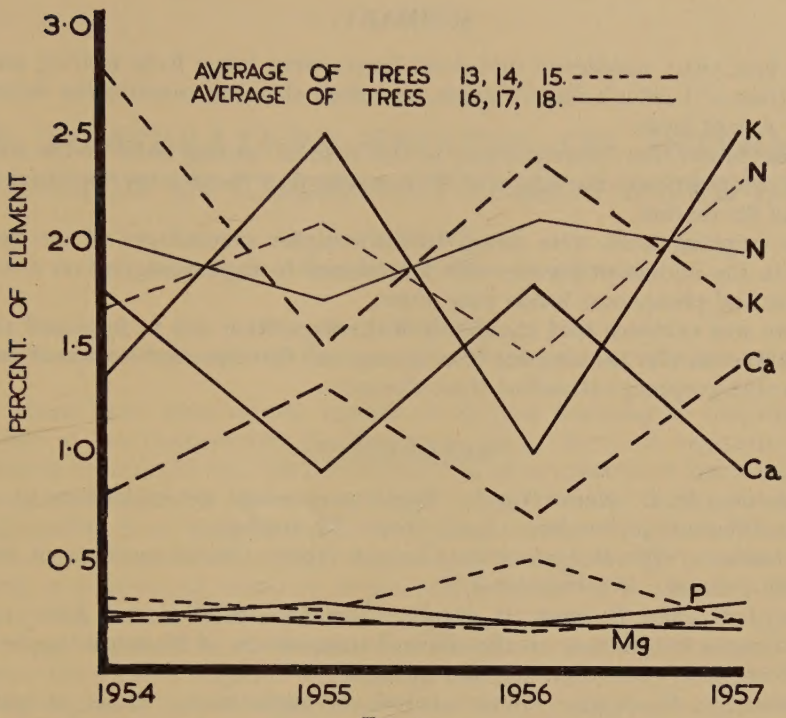

FIG. 1.

Biennial fluctuation in nutrient status of apple leaves as related to biennial bearing; "off" years for trees 13-15 in 1954 and 1956, for trees 16-18 in 1955 and 1957.

noticeable in this orchard. This increase of magnesium in the foliage of bearing trees may be a secondary effect, consequent on the lowering of leaf potassium, rather than a direct effect due to the crop.

Contrary, however, to the findings of Cain and Boynton, total bases (Ca+Mg+K) show a tendency, sometimes marked, to decrease with cropping and with increased nitrogen application. The decrease in potassium due to the crop is generally such as to outweigh the increases in calcium and magnesium.

Mason, working with the biennial variety Miller's Seedling under clean cultivation in England, also found higher concentrations of nitrogen, magnesium, manganese and calcium in the bearing trees (5). His results differ, however, from those reported here (and from those of Cain and Boynton, whose trees were under grass) in that he found higher phosphorus in the bearing trees and did not find any significant differences for potassium. In Connecticut, Emmert (4) found that leaves from bearing trees of the variety Baldwin were lower in potassium and phosphorus, but higher in nitrogen and calcium, than non-bearing trees in the same orchard.

Though statistically significant evidence for the effects of increased nitrogen nutrition on the foliage of these Laxton's Superb trees is available only for the year 1954, the indications are that these effects are in the directions reported by Cain and Boynton for the variety McIntosh Red, and that they resemble those due to the presence of a crop.

SUMMARY.

For four years samples of mid-shoot leaves were taken from bearing and non-bearing trees of Laxton's Superb apple, and their chemical constitution determined on a dry weight basis.

It was found that, corresponding to the biennial-bearing habit of the trees, the chemical composition of the foliage at the sampling date (September–October) showed a biennial fluctuation.

The cropping trees were found to have higher percentages of nitrogen and calcium in the mid-shoot leaves, with a tendency to higher magnesium also. The potassium and phosphorus levels were lower.

There was evidence that changes in leaf composition due to increased nitrogen nutrition were similar to those due to cropping, and that the combination of increased nitrogen with cropping intensified these changes.

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LOW TEMPERATURE EFFECTS ON INTERNODE EXTENSION IN *CHRYSANTHEMUM MORIFOLIUM*

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WHILE there have been several reports of delayed flowering in *Chrysanthemum morifolium* at low temperatures (Cathey, 1954, 1955), effects on vegetative growth have largely been neglected. The development of basal rosettes at low temperatures was recorded in 1938 by Roberts and Struckmeyer for the variety Lilian Doty, but apparently these authors did not continue their investigation. The present experiments were undertaken following several observations of rosetted growth occurring in commercial nurseries under low temperature conditions during the winter months in both U.S.A. (Miller, 1956) and England. One observation of this kind was made on a nursery in Sussex where plants were growing in a newly erected glasshouse temporarily unglazed at the ends; a marked gradation in height from the cooler ends towards the warmer centre occurred in the early stages of growth.

A study of the effects of low temperature on the vegetative growth habit was considered to be of particular interest in view of the similar reduction in internode length with the development of a rosette habit, which occurs under high temperature/short-day conditions in non-vernalized plants (Schwabe, 1950).

Experimental Material and Methods

Except where otherwise stated, all cuttings used in the following experiments were shoot tips from vernalized stock plants, so that they were already fully vernalized at the beginning of the experiments (Vince, 1957). In this way the direct effect of temperature on internode elongation could be studied.

It was not found possible to replicate the day-length and temperature treatments. In experiments 1 and 3 these treatments were given between 4 p.m. and 8 a.m. in controlled environment rooms where positional effects were likely to be small; between 8 a.m. and 4 p.m. the plants in all treatments occupied randomized positions in the same glasshouse. A day temperature minimum of 60°F. was maintained but the maximum was uncontrolled and varied with the time of year.

In experiments 2 and 4 the temperature treatments were given in separate glasshouse compartments involving, in experiment 2, transfer from one to the other for the varying periods of treatment; positional effects may, therefore, have been larger.

Unless otherwise stated, the long-day treatments consisted of 8 hours daylight with 9 hours of supplementary low-intensity light; short photoperiods consisted of 8 hours of daylight.

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Plants were grown at Reading, except those in experiment 2 which were grown at Ithaca, New York.

RESULTS.

Experiment 1. Effect of night temperature and day-length on internode extension.

Cuttings of the variety Mayford Crimson were taken on 17th July 1957 and were rooted and grown at 60°F. in long days. The plants were cut back to five leaves on 20th August and the treatments listed in Table I commenced. Two laterals were allowed to develop on each of five plants, giving ten replicate shoots in each treatment. The long-day treatment continued for 52 days until October 11th, when the plants were transferred to short days. The experiment was terminated on 22nd November after a further 41 days.

TABLE I.

Effect of night temperature and day-length on mean internode length; variety Mayford Crimson.

Night temperature (°F.)		Mean internode length (cm.)	
In long days	In short days	In long days (20th Aug. to 11th Oct.)	In short days (11th Oct. to 22nd Nov.)
60 (15·5°C.)	60	2·2	1·2
60	50	2·1	1·0
50 (10°C.)	60	1·5	1·1
50	50	1·4	0·5
In short days throughout		In short days (20th Aug. to 11th Oct.)	
60		1·9	
50		1·2	
Significant difference at P = 0·05		0·20	0·22

The mean internode lengths for the long-day period were calculated from the total length of each shoot and the total number of expanded leaves on 11th October. Similarly the mean internode lengths for the short-day period were calculated from the length of each shoot measured from the last leaf expanded on 11th October, and the number of expanded leaves from this point.

The lengths of individual internodes were also measured at the end of the experiment ; data for the sixth internode from the base of the shoot, and for the third and sixth internodes counted from the last expanded leaf at the time of transfer to short days, are illustrated in Fig. 1.

At the end of the experiment (on 22nd November) shoots at 60°F., given short days following long days, showed normal elongation and were in bud ; shoots at 60°F. in short days throughout were in full bloom. Shoots at 50°F. in short days had become very variable ; four shoots were extremely rosetted, whereas three showed considerable stem extension and had budded. The remainder showed some elongation. Shoots at 50°F., given short days following long days, were uniform and

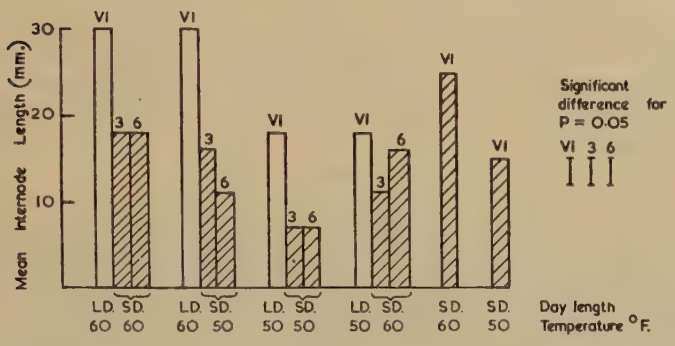

FIG. 1.

Effect of changes in temperature and day-length on internode elongation; variety Mayford Crimson.

VI; Sixth internode from the base of the shoot.
3, 6; Third and sixth internodes counted from the last expanded leaf at the time of transfer to short days.

showed very marked vegetative terminal rosettes. These effects are illustrated in Fig. 2.

It is apparent from Table I that, in plants at 60°F. or 50°F. throughout, mean internode length was less at the lower temperature in both long and short photoperiods; the effect of temperature appears to be independent of and additive to that of day-length. Although a greater reduction in internode length occurred when short days followed a period in long days, the difference between temperature treatments was maintained. Following transfer from 50°F. to 60°F., mean internode length (for the S.D. period) increased compared with plants at 50°F. throughout; following transfer from 60°F. to 50°F., mean internode length (for the S.D. period) did not differ significantly from plants at 60°F. throughout.

The effects of transferring plants from high to low temperature and vice-versa are shown in more detail in Fig. 1. Following transfer from 60°F. to 50°F., the third internode from the last leaf expanded at the time of transfer showed a slight but non-significant reduction in length compared with that of plants grown continuously at 60°F.; for the sixth internode the reduction in length at 50°F. was significant. Following transfer from 50°F. to 60°F., both the third and sixth internodes showed a significant increase in length compared with those of plants grown continuously at 50°F.; the length of the sixth internode did not, in fact, differ significantly from that in plants kept at 60°F. throughout.

These results show that transfer from low to high temperature brings about a more immediate response than one from high to low temperature.

Experiment 2. Internode elongation following transfer from high to low night temperature.

Rooted cuttings were potted on 2nd January 1957 (vars. Cordova and Citation on 7th January). The following American varieties were grown: Bluechip, Cordova, Citation, Golden Herald, Garnet King, Lilian Doty, Indianapolis White, Minstrel and Shasta. Plants were grown at 65°F. in long days until 24th January,

when they were given 0, 4, or 8 weeks at 50°F. night temperature and subsequently transferred again to 65°F. Each set of temperature treatments was given in long days (natural days with supplementary light from tungsten-filament lamps from 10 p.m. to 2 a.m.) and in short days. Plants were measured at the beginning of the experiment on 24th January and again after eight weeks ; data for total height and number of expanded leaves on the stem were obtained.

The calculated values for mean internode lengths (stem length divided by number of expanded leaves) are compared in Fig. 3. Three points of interest emerge. Firstly,

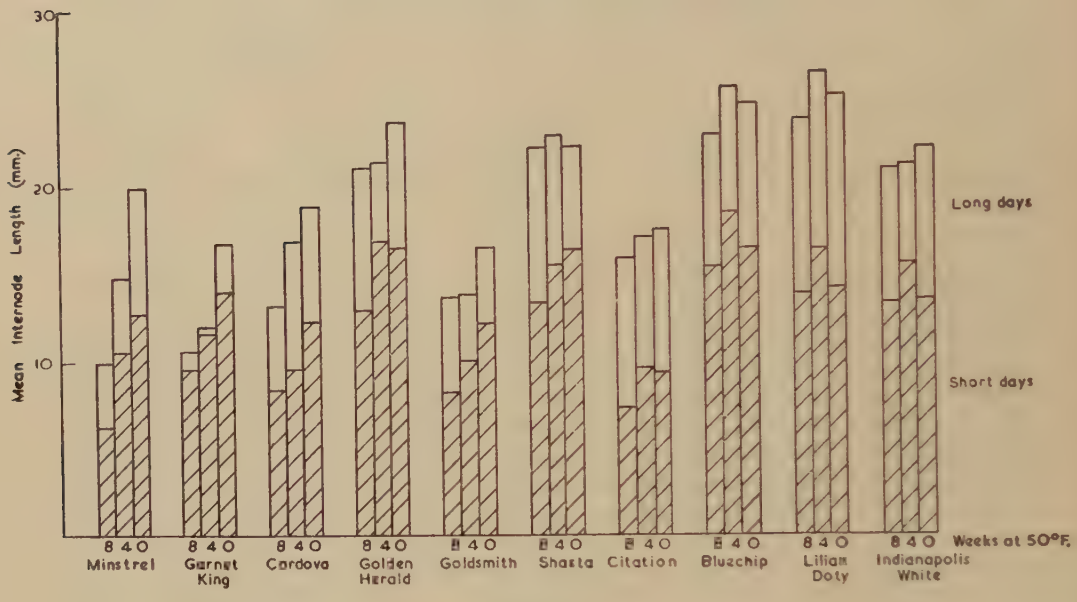

FIG. 3.

Effect of temperature and day-length on mean internode length, showing internode elongation following transfer from low to high temperature.

the effect of temperature again appears to be largely independent of day-length effects ; mean internode length was, with one exception, less in short than in long days and in general the effect of low temperature was additive to that of short days. Secondly, whereas the magnitude of the day-length effect was similar in all varieties (except Garnet King), there was considerable variation in the response to low night temperature. The greatest reduction in internode length occurred at low temperature in Minstrel and Garnet King, whereas Indianapolis White and Blue Chip showed little, if any, effect. Surprisingly Lilian Doty also showed almost no response (see Roberts and Struckmeyer, 1938). Thirdly, the rapid increase in internode length following transfer from low to high temperature is again apparent. The experimental values represent mean internode lengths calculated for the entire shoot, so that the increase in length of the internodes developed after transfer was greater than these mean values would indicate.

PLATE I.

Fig. 2.

Rosetted growth at low temperature ; variety Mayford Crimson.
Left to right : 60° F. (S.D. following L.D.); 60° F. (continuous S.D.); 50° F. (continuous S.D.); 50° F. (S.D. following L.D.).

[*face page 202*

PLATE II

FIG. 4.

Rosetted growth following transfer from high to low temperature; variety Mayford Crimson. Left to right: L.D. 60°, S.D. 60°; L.D. 60°, S.D. 50°; L.D. 50°, S.D. 50°; L.D. 50°, S.D. 60°. (Temperatures in °F.).

Experiment 3. Effect of low night temperature at different stages of growth on internode extension.

Two experiments primarily designed to investigate the effect of low temperature on flowering, and which will be reported in greater detail in a later paper, furnished some data on the effects of low night temperature on internode elongation which may be considered here.

Experiment 3a.

A combination of two different low night temperature treatments (40°F. and 50°F.) with one high temperature treatment (60°F.) was set up. Rooted cuttings were grown in long days at 60°F. for one week until 10th October 1955, when they were cut back and the temperature treatments listed in Table II begun. One shoot only was allowed to develop on each plant. The long photoperiods were continued until 18th November, when the plants were transferred to short days. Four replicate plants of each of the varieties Mayford Crimson, Crensa and Balcombe Perfection were grown in each treatment.

Plants were measured at the end of the long-day period and again at anthesis or, in the case of those plants not reaching anthesis, at the end of the experiment in August 1956. The lengths of the lateral shoots and the numbers of leaves were recorded ; the mean internode lengths were calculated from these data.

At the end of the long-day period on 18th November 1955, mean internode lengths in all varieties showed some reduction at low compared with high temperatures (Table II). The differences between 60°F. and 50°F. were small but the reduction in internode length at 40°F. in Balcombe Perfection and Mayford Crimson was considerable.

Following the transfer to short days, differences in growth became apparent during December and, by January 1956, the differences between treatments were very marked. The following observations were made on 22nd February :

Mayford Crimson (Fig. 4.) Plants grown at 60°F. throughout had reached anthesis. Plants transferred to 50° or 40°F. following long days at 60°F. showed marked terminal rosettes with dark bluish-green foliage. Plants grown at 40° or 50°F. throughout were vegetative but no obvious terminal rosettes were present; leaves were less blue than in plants transferred from 60°F.

Balcombe Perfection. Plants grown at 60°F. throughout had reached anthesis. Plants transferred to 40°F. following long days at 60°F. showed terminal vegetative rosettes ; plants transferred to 50°F. were in bud, except for one which had rosetted. Plants at 40°F. throughout were vegetative but no marked rosettes had formed.

Crensa. Plants at 60°F. throughout were in bud. Plants transferred to 50° or 40°F. following long days at 60°F. showed marked terminal vegetative rosettes with bluish-green foliage. The leaves on the rosette were more deeply dissected than is usual and the lobing was more acute, especially at 40°F.

With all three varieties, stem diameter increased and the stem became very succulent when a rosette was formed. The greatest degree of visual rosetting occurred in plants transferred from high temperatures in long days to low temperatures in

TABLE II.

Effect of night temperature at different stages of growth on internode length.

Night temperature °F.		Mayford Crimson			Crensa			Balcombe Perfection		
During L.D.	During S.D.	Mean internode length (cm.)			Mean internode length (cm.)			Mean internode length (cm.)		
		18th Nov.*	24th Feb	Final	18th Nov.*	24th Feb.	Final	18th Nov.*	24th Feb.	Final
60	60	1·30		1·79	1·29		1·02	1·06		0·94
60	50	1·37	1·14 (0·36†)	1·42	1·15	0·83 (0·49†)	1·55	1·10	0·89	1·54
60	40	1·25	1·02 (0·33†)	1·09	1·25	1·02 (0·47†)	1·30	1·03	0·91 (0·45†)	1·54
60 (15·5°C.)	60‡	1·30		1·79	1·29		1·02	1·06		0·94
50 (10°C.)	60	1·03		1·45	1·34	0·70	1·10	0·87		1·03
40 (4·5°C.)	60	0·49		1·30	0·85	0·70	0·98	0·55		0·96
60	60‡	1·30		1·79	1·29		1·02	1·06		0·94
50	50	1·15	1·13	1·62	1·21	1·00	1·63	1·01	1·16	1·86
40	40	0·61	0·90	1·31	1·07	1·02	1·49	0·65	1·01	1·60
Significant Difference at P = 0·05		0·22		0·22	0·23		0·26	0·20		0·21

* End of long-day period.
† Mean internode length of terminal rosette.
‡ Data repeated for ease of comparison.

short days. This may have been partly due to a greater contrast following maximum internode length at high temperature during long days but this cannot be the entire explanation, since differences between 50°F. and 60°F. at the end of the long-day period were small. Following these visual observations, stem lengths and leaf numbers of vegetative plants were obtained on 24th February ; where plants had developed a marked terminal rosette, the beginning of which could be determined accurately, data were also obtained from the rosetted portion alone. These rosettes consisted of 15-20 expanded leaves and, therefore, contained a high proportion of fully expanded internodes ; the mean internode lengths for the rosettes (which ranged from 0·33 to 0·49 cm.) can thus be considered to be reasonably accurate estimates of the final internode lengths attained during this period of growth at low temperature.

In Mayford Crimson the final mean internode lengths at anthesis, or at the end of the experiment in August 1956, showed significant reductions at 50° and 40°F. compared with 60°F. In Balcombe Perfection and Crensa, however, plants receiving low temperatures during short days showed an increase in final mean internode length compared with plants receiving 60°F. during short days. Thus in these varieties, during continued low temperature treatment in short days, the later-formed internodes must have elongated considerably more than those formed earlier. All plants flowered except Crensa and Mayford Crimson given 40°F. during short days.

Experiment 3b.

The varieties listed in Table III were grown at 50° or 60°F. night temperatures. Cuttings were rooted and grown in long days at 60°F. ; the plants were cut back on 11th September 1956 when the temperature treatments began. Long days continued until 27th October when the plants were transferred to short photoperiods. Five replicate plants of each variety were grown in each treatment ; only one lateral shoot was allowed to develop on each plant. The experiment was discontinued on 8th July 1957 by which time all plants had formed buds.

TABLE III.

Effect of prolonged exposure to low night temperature on mean internode length.

Variety	Mean internode length (cm.)			
	At end of long-day period, 27th Oct. 1955		At anthesis or end of experiment in July 1956	
	60°F. (15·5°C.)	50°F. (10°C.)	60°F.	50°F.
American Beauty	2·3	1·8	2·3	1·9
Balcombe Perfection	1·2	0·6	1·0	1·8
Encore	1·4	1·0	1·4	2·0
Friendly Rival	1·6	1·2	1·3	2·0
Fred Shoesmith	1·6	1·2	1·7	2·0
Gordon Wells	1·6	1·5	1·8	2·0
Rose Harrison	2·3	1·4	1·9	2·3
Crensa	1·5	1·0	1·7	1·7
Mayford Crimson	1·4	0·7	1·2	1·7
Worthing Success	1·0	0·7	1·2	1·3

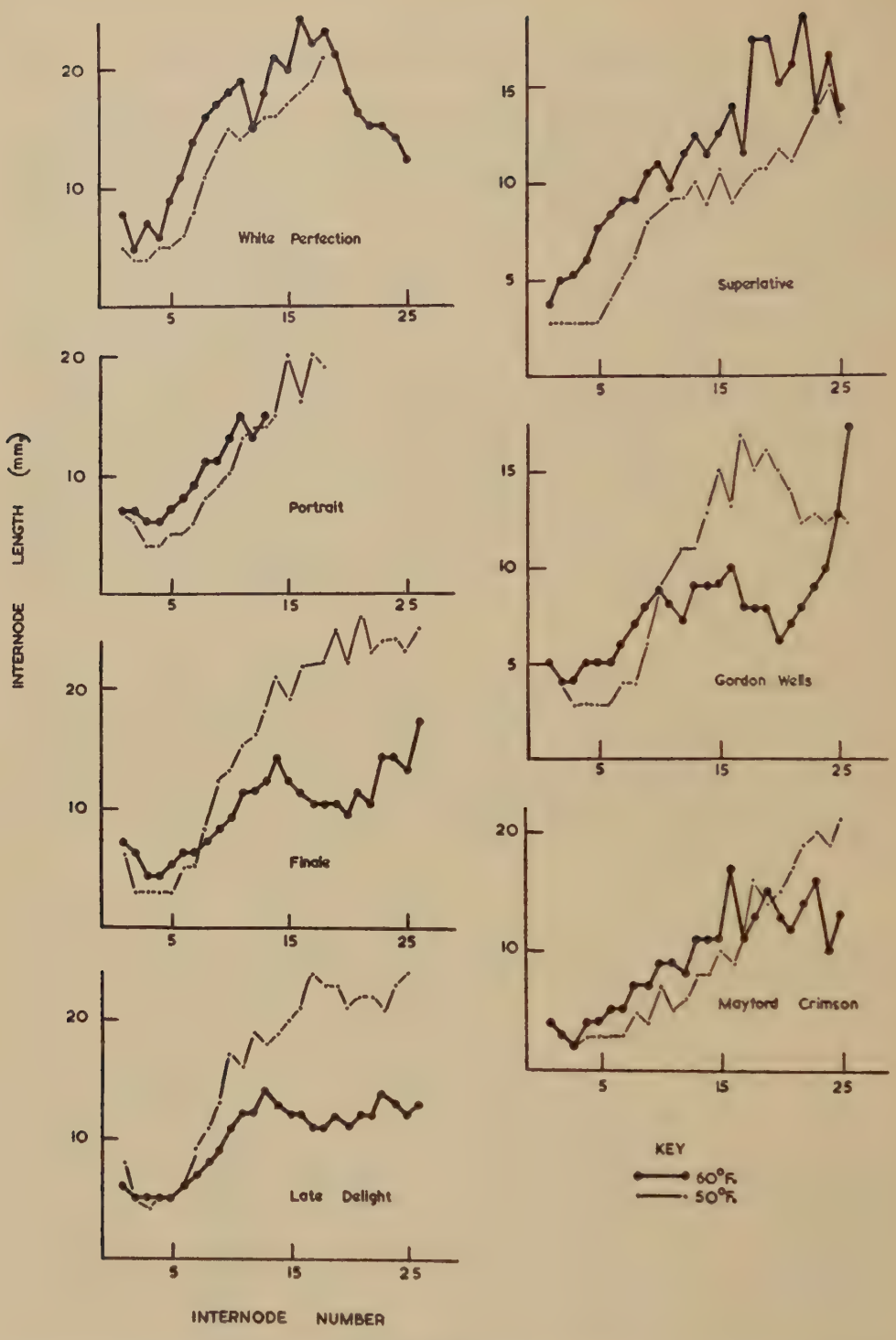

FIG. 5.

Effects of temperature on internode length in short days; internode number counted from the base of the plant.

At the end of the long-day period all varieties showed a decreased mean internode length at 50°F. compared with 60°F. In all varieties except American Beauty and Crensa, however, the final mean internode length was greater at 50° than at 60°F. As in the previous experiment, therefore, continued growth in short days at 50°F. resulted in increased elongation of the later-formed internodes, even though initially (in this case during the long-day period) internode length was less at 50° than at 60°F.

In view of the results of these two experiments a further experiment was carried out in which the lengths of individual internodes were measured.

Experiment 4. Effect of temperature on length of individual internodes.

In this experiment basal cuttings were allowed to develop on stock plants kept at low temperatures (mean minimum night temperature 51°F.) in natural short days after flowering. Cuttings of several varieties (see Fig. 5.) were rooted at 60°F. in long days. Ten rooted cuttings of each variety in each temperature treatment were potted and returned to short photoperiods on 21st Februrary 1958. The mean minimum night temperatures (4 p.m. to 8 a.m.) in the two temperature treatments were 47·5°F. and 59·1°F. respectively. Temperature differences during the day were smaller ; mean maximum temperature differences were 5 to 7°F. from February to April, and there were no differences in May and June. The experiment was terminated in June by which time all varieties in high temperatures were in bud, showing colour, or had reached anthesis ; at the lower temperature only Late Delight and some plants of Portrait had formed visible buds.

In general some reduction of internode length occurred at the lower temperature during the early stages of growth in short days but, with the exception of White Perfection and Superlative, the later-formed internodes were longer at low than at high temperatures (Fig. 5). The degree of reduction at low temperatures was rather small, being of the order of 0·3 cm. in most varieties and 0·6 cm. in White Perfection.

DISCUSSION.

During the early stages of growth in long or short photoperiods, or immediately following transfer from long to short days, the final length attained by the internodes was reduced at low night temperature (50°F. or below) when compared with 60°F. Internode length was also reduced in short compared with long photoperiods. Temperature and day-length appeared to act to a large extent independently and, consequently, maximum reduction in internode length with the development of a rosette habit occurred at low temperatures only in short days. Unlike the effect of day-length, which occurred in all varieties tested, the effects of low temperature varied and affected only some varieties to any appreciable extent. So far true rosetting at low temperatures has only been found to occur in those varieties which require vernalization and which form rosettes if grown without chilling in high temperature/short-day conditions (examples are Mayford Crimson, Balcombe Perfection and Dora Ramsay). The significance of this apparent correlation is obscure, but it is possible that, under natural conditions when vernalization is complete, elongation of the overwintering rosette is thus prevented until higher temperatures occur in the early summer. Certainly internode extension is rapidly resumed when the "low-temperature rosette" is returned to high temperatures.

Although internode length was reduced at low temperatures during the early stages of growth, in some experiments the later-formed internodes elongated more in the low than in the high temperature treatments. Three possible explanations may be considered. Firstly, the increase in length of the later-formed internodes may have been related to bud formation. Heslop-Harrison (1957) has suggested that short days decrease the stem extension during vegetative growth but may actually increase stem extension once flowering has occurred; a similar possibility may occur here in that the mechanism governing stem elongation may alter, once bud initiation has occurred. Secondly, in each of the experiments in which this phenomenon occurred, the treatments continued into the summer and the increased length of the later-formed internodes may have occurred as a result of high day temperatures following the early period of low temperature. A period of low temperature during vegetative growth has been shown to cause a subsequent increase in internode length at high temperatures, even in those varieties with no low temperature requirement for flowering (Mason, 1957). Thirdly, it is possible that reduced utilization of substrates during the early period of growth may have resulted in an increased availability, with a consequent increase in internode length, when the higher day temperatures were more favourable for elongation.

SUMMARY.

A low night temperature was found to have a marked influence on internode length in *Chrysanthemum morifolium*, but the effect varied and depended on variety and stage of growth.

During the early stages of growth, or immediately following transfer from long to short days, internode length was reduced at 50°F. (10°C.) or below as compared with 60°F. (15·5°C.). Some varieties, however, showed little response. Internode length was also reduced in short days as compared with long days, and the effects of temperature and day-length appeared to be largely independent. Consequently the greatest reduction in internode length, with the development of a rosette habit, occurred only in short days.

Following the extended period of growth in short days, however, the later-formed internodes elongated more at low than at high temperatures.

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EFFECTS OF ENVIRONMENT ON *RUBUS IDAEUS* L.

III. GROWTH AND DORMANCY OF YOUNG SHOOTS

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In the first two papers of the present series the general morphology and growth habit of the young raspberry shoot were described in detail (Hudson, 1959 ; Williams, 1959). It was shown that a root sucker appearing above soil level in the autumn forms a rosette of leaves a few centimetres above soil level and then passes through the first winter in a dormant state. In the following spring the apical meristem resumes active elongation and a vegetative shoot develops. This shoot may attain a height of two metres or more before it ceases elongation and again becomes dormant in the second autumn. The present paper describes experiments in which a series of growth rooms and a cool glasshouse were used to study the influence of the environment upon the elongation and dormancy of newly emergent root suckers.

Material and methods.

The variety Malling Promise was used. Plants were propagated from root cuttings and prior to growth-room studies were grown in a cool glasshouse. During this period care was taken to keep them in an actively growing condition. A day-length of 16 hours was maintained, using high pressure mercury vapour lamps to extend the natural day-length where necessary, and temperatures were not allowed to fall below 55° F. The growth rooms consisted of three insulated rooms in which light was provided by mobile racks of " daylight " fluorescent lamps giving a light intensity of 450–500 foot candles at the leaf surface. Temperatures could be maintained at any level between 30° and 70° F. to within about 2° F. For studies concerned with low temperatures a large refrigerator was used. Fuller details of these growth rooms have been published elsewhere (Hudson and Williams, 1957).

Results.

Onset of dormancy.

Plants were grown in a cool glasshouse until they had developed two or three fully expanded leaves and were between one and two centimetres high. Groups of 48 plants were then moved into each of the three growth rooms and each group sub-divided for two treatments. The conditions of day-length and temperature may be summarized as follows :

No. of plants	*Temperature*	*Day-length*
24	70° F. (21° C.)±2°	9 hrs.
24		14 hrs.

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24 24	}	60° F. (15·5° C.)±2°	{ 9 hrs. 14 hrs.
24 24	}	50° F. (10° C.)±2°	{ 9 hrs. 14 hrs.

Elongation (Figs. 1 and 2). At 70° F. plants continued to elongate throughout the experiment, in both the long-day and the short-day treatment. Although there was less elongation in the latter, this was probably a quantitative effect and these plants did not appear at any stage to be becoming dormant.

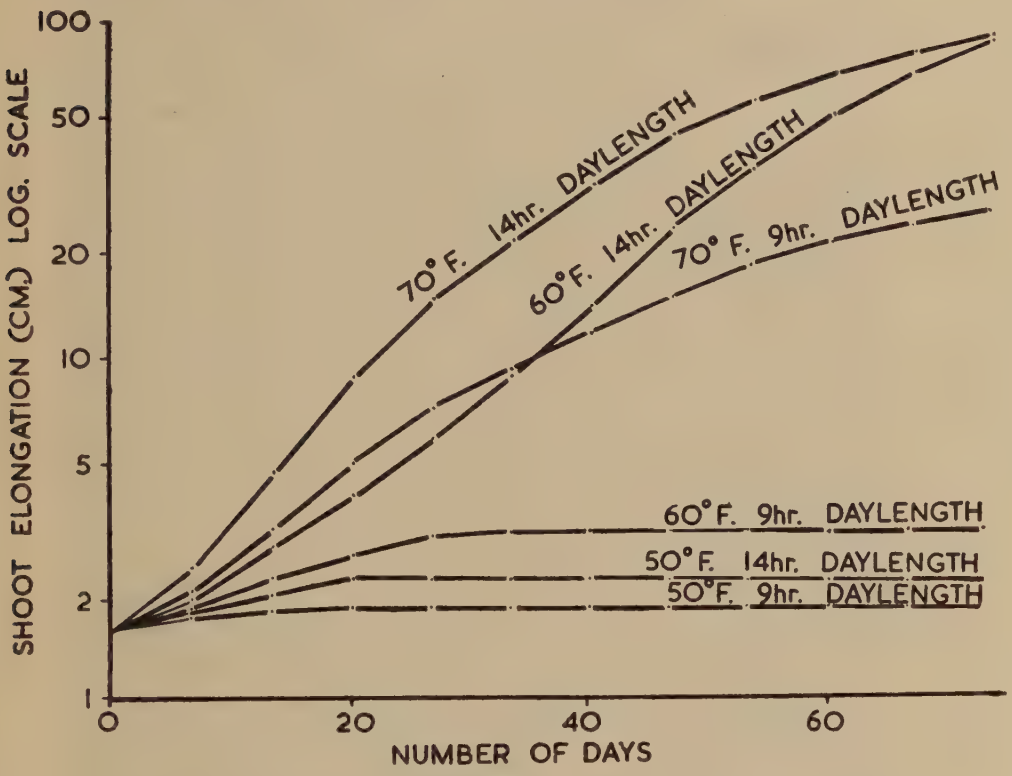

FIG. 2.

Elongation of shoots (mean of 24 plants) under different environmental conditions.

At 60° F. plants in the long-day treatment elongated consistently. In marked contrast, plants in the short-day treatment ceased any measurable elongation within about five weeks. The rate of elongation declined fairly rapidly and a typical rosette of leaves developed round the apex. At 50° F. little elongation occurred either in long or in short days, although slightly more in the former than in the latter.

Leaf development (Fig. 3). The number of leaves which developed in the various treatments followed a similar course to that of shoot elongation. New leaves

developed throughout the experiment at 70° F. in both long and short days and at 60° F. in long days. In short days at 60° F., and in both daylengths at 50° F., the number of expanding leaves decreased, new leaves ultimately ceased to appear, and successively developing leaves became smaller, with shorter petioles and smaller areas of lamina. Leaves continued to expand for some time after shoot elongation had ceased, giving rise to the characteristic form of the leaf rosette surrounding the apical portion of the shoot. The behaviour of plants within each treatment was uniform.

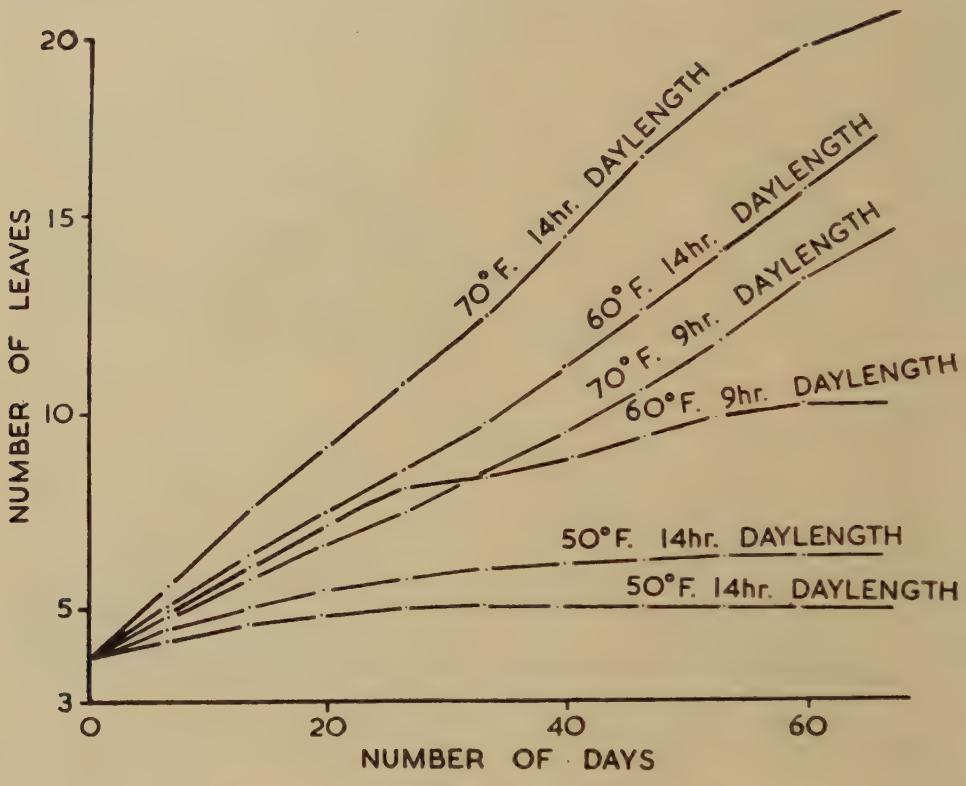

FIG. 3.
Number of leaves which developed under different environmental conditions.

Axillary bud development. In the treatments in which plants continued to elongate, axillary buds remained small and were largely enclosed within the bases of the leaf petioles. In those treatments in which shoots became dormant there was at the same time a marked increase in the size of axillary buds (Fig. 4). This increase was most evident in the buds just at or below soil level.

Duration of the onset of dormancy.

In an earlier experiment, described fully elsewhere (Hudson, 1955), it was noted that root suckers which had been dormant for varying periods differed in the manner

PLATE I

Fig. 1.

Elongation of raspberry plants under different environmental conditions.

A Grown at 70° F. in a 14 hr. day-length.
B " 70° F. " 9 hr. "
C " 60° F. " 14 hr. "
D Grown at 60° F. in a 9 hr. day-length
E " 50° F. " 14 hr. "
F " 50° F. " 9 hr. "

[*face page 212*

FIG. 4.

Conspicuous swelling of axillary buds in root suckers which have become dormant.

FIG. 5.

Development of a replacement bud (*left*) from the base of a rosetted dormant shoot (*right*), which has not recommenced to elongate.

A B C

D

E

FIG. 7.

Effect of natural winter conditions upon the breaking of dormancy of root suckers. Plants photographed at the beginning of February 1957.

A Plant placed in heated glasshouse in the first week of Sept. 1956.
B " " " " " " " Oct. 1956.
C " " " " " " " Nov. 1956.
D " " " " " " " Dec. 1956.
E Plants arranged for direct comparison.

in which growth was resumed. In the experiment now being reported it was possible to observe the behaviour of shoots emerging from batches of root cuttings placed in a cool glasshouse each month from September to January. No artificial light was used so that the plants were grown in the natural short days of autumn and the lengthening days of early spring. Shoots which emerged from September to December became dormant after making very little growth above soil level. In all cases growth was resumed in late February, but elongation of shoots from the earlier batches, i.e. those in which shoots had emerged in September and October, was not from the apical meristem of the original shoot, but by the rapid elongation of an axillary bud close to soil level (Fig. 5). Shoots which had emerged in November and December, although these had formed rosettes and appeared to have become fully dormant, resumed growth by the activity of the original apical meristem.

It is possible that the onset of dormancy is a gradual process, reversible in its early stages, but that a stage is reached when dormancy is complete and the apical meristem is unable to resume active growth under conditions of rising temperatures and lengthening days. Under these conditions an axillary bud elongates instead. The next experiment was designed to examine the effect of the length of the period of dormancy upon the subsequent manner of elongation.

Plants were grown under long days in the glasshouse until they were about ten centimetres high and were elongating vigorously. They were then moved into a growth room maintained at 50° F. with a 9-hour day-length. At intervals of two weeks 24 plants were transferred to a growth room maintained at 70° F. and a 16-hour day-length. In this way it was possible to observe the effect of successively longer periods of apparent dormancy upon the subsequent manner of development.

Although growth ceased and rosettes developed in all plants in the cooler environment, in earlier groups the apical meristem resumed direct elongation when moved to conditions of long days and high temperatures. The majority of plants which received eight to ten weeks of cool temperature and short days behaved in this manner although, in a few cases, an axillary bud grew out and the original shoot remained dormant. Thereafter, removal to the higher temperature and longer days invariably resulted in the development of an axillary bud only (Table I). A group of control plants, grown at 70° F. and in a 16-hour day-length throughout the experiment, continued to elongate.

Breaking of dormancy.

Resumption of growth of root suckers in the spring by the development of an axillary bud, instead of from the apex of the original shoot, was never observed in the field. Those which appeared in the autumn resumed growth in March or April by renewed activity of the original apical meristems. Yet these suckers had been dormant for a considerably longer period than those in the growth-room experiment described above and it seemed likely that, in common with many temperate shrubs, a period of lower temperature was necessary to break dormancy once this state was fully established.

Vigorously elongating plants were first placed in a growth room maintained at 50° F. and a 9-hour day-length, where they remained for a period of sixteen weeks. On the basis of the previous experiment this was considered a sufficiently long period to ensure that the plants had become completely dormant. The plants were then transferred to an unlit refrigerator at a temperature of 38° F. At intervals of two

TABLE I.

Effect of cool temperature and short days upon the onset of dormancy and subsequent growth. Total of 24 plants in each group.

No. of weeks plants were grown in a day-length of 9 hr. at 50° F. (10° C.)	No. of plants which elongated directly when transferred to a day-length of 16 hrs. at 70° F. (21° C.)	No. of plants in which an axillary bud developed when transferred to a day-length of 16 hrs. at 70° F. (21° C.)
2	24	0
4	24	0
6	24	0
8	23	1
10	21	3
12	0	24
14	0	24
16	0	24
18	0	24
20	0	24

weeks, twelve plants were transferred to a growth room at 70° F. and a 16-hour day-length to determine the influence of successively longer periods of low temperature upon the behaviour of the terminal meristems of the shoots of dormant plants.

Two weeks at 38° F. failed to break the dormancy of the apical meristems and plants returned to conditions of 70° F. and long days resumed growth by the elongation of an axillary bud. After four and six weeks of low temperature an increasing number of plants resumed growth by the apical meristem of the original shoot. After a period of eight weeks or more of low temperatures all plants resumed growth in this manner. (Table II.)

TABLE II.

Effect of low temperature on the breaking of dormancy. Total of 12 plants in each group.

No. of weeks plants were grown in a day-length of 9 hrs. at 50° F. (10° C.)	No. of weeks plants were grown at 38° F. (3·3° C.)	No. of plants which elongated directly when transferred to a day-length of 16 hrs. at 70° F. (21° C.)	No. of plants in which an axillary bud developed when transferred to a day-length of 16 hrs. at 70° F. (21° C.)
16	2	0	12
16	4	5	7
16	6	10	2
16	8	12	0
16	10	12	0
16	12	12	0
16	14	12	0

Duration of dormancy under natural conditions.

Observations were made on the influence of successively longer periods of natural autumn and winter conditions upon the resumption of growth of dormant root suckers which were still part of the parent plant (unlike the plants grown from root cuttings, used in the growth-room experiments).

The parent plants were grown in a cool glasshouse from February to June 1956 by which time each of them had developed a strong vegetative shoot about 1½ metres in height. During this period of vigorous elongation of the primary shoot no root suckers appeared. In mid-June the plants were finally potted into 10-inch pots and were placed in the open, the pots being partially buried in ashes. Elongation of the primary shoot continued until August, by which time the plants were about two metres in height.

Concurrent with the cessation of growth of the primary shoot a large number of root suckers began to appear above soil level, each developing a typical rosette of leaves and remaining close to the soil.

From September onwards, at two-weekly intervals, six plants were returned to a cool glasshouse, in which no artificial illumination was given, and the temperature was not allowed to fall below 50° F.

Root suckers on plants housed in September and October made no growth until late January, when very slow elongation began and a small number of new leaves developed. Plants brought into the glasshouse at the beginning of November also remained dormant until late January, as in the previous batches, but those housed at the beginning of December behaved differently, growth being resumed within a few days of the plants being brought into the glasshouse (Fig. 6).

Subsequent groups behaved in a similar manner to those brought in at the beginning of December. The apical meristems became active, new leaves developed and all root suckers began to elongate within a few days. The more rapid rate of elongation of plants which had successively longer periods of natural winter conditions before being brought under glass is shown in the photographs taken in early February (Fig. 7).

DISCUSSION.

In their early studies of the photoperiodic responses of plants Garner and Allard (1923) drew attention to the fact that length of day could influence the rate of elongation of plants. They went further to suggest that this was " a fundamental phenomenon underlying the various other (photoperiodic) responses including flowering and fruiting ". Subsequent studies were, however, largely concerned with the relationship between day-length and flower initiation. More recent studies of the dormancy of a wide range of temperate woody shrubs and trees have shown that, in many cases, the onset of dormancy (which generally involves the cessation of elongation, leaf abscission and the formation of some form of resting buds) can be induced by growing plants under short-day conditions. Similarly, the resumption of active growth must generally be preceded by a period of low temperatures or " chilling " in the region of 40° F. (Kramer, 1936 ; Van der Veen, 1951 ; Downs, 1955). These aspects have recently been reviewed by Wareing (1956).

The present series of experiments has shown that, with this variety of raspberry, climatic conditions largely govern the behaviour of the emergent root sucker. In the

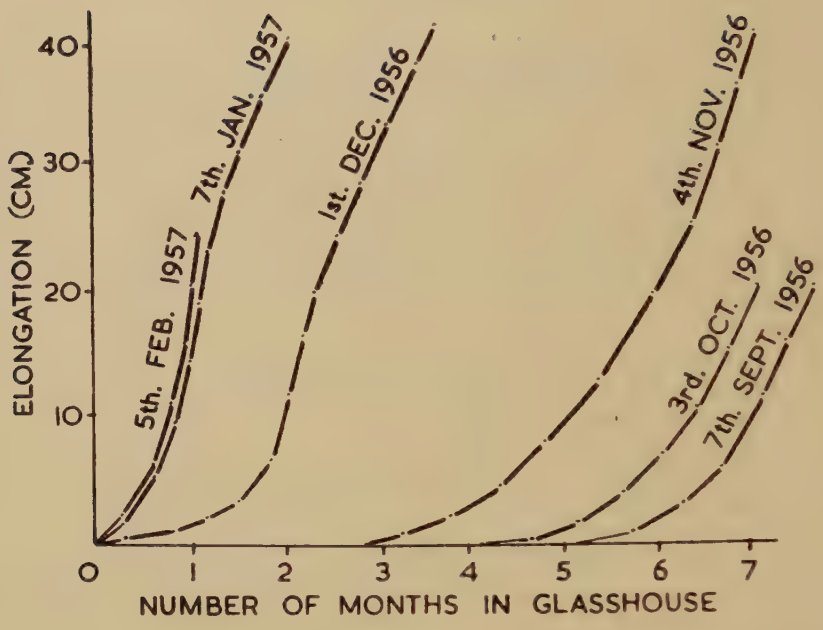

FIG. 6.

Effect of natural winter conditions upon the breaking of dormancy and subsequent growth of root suckers. Each curve shows the mean growth of 36 root suckers from six plants, taken into a heated glasshouse on the dates indicated.

field the shortening days and falling temperatures of autumn bring about the onset of dormancy, when the rate of elongation rapidly declines. Growth-room experiments indicate that the onset of dormancy is a gradual process, extending over a number of weeks, and is reversible in its early stages if the plants are returned to conditions of long days and higher temperatures. A stage is reached when dormancy is not readily reversed and the shoot may be regarded as fully dormant. This state of dormancy can, however, be broken by a period of low temperatures, a process in which light does not appear to be essential, since under growth-room conditions a period of about six weeks at 38° F. without light was effective. In the field, low winter temperatures gradually remove the effect of dormancy and the experiment in which pot-grown plants were brought under glass in successive batches showed that, in 1956, dormancy of the root suckers was ended by early December. Since root suckers in the open do not resume active growth at this time it would seem that, after the dormancy requirements are satisfied, shoots are prevented from growing by the low temperatures usually experienced in early spring. With the onset of warmer conditions in the spring, growth is readily resumed. The second flush of root suckers which appears at this time (Williams, 1959), together with those which have passed through the winter as dormant shoots, enter a period of elongation which is sustained throughout the early summer by the long days and higher temperatures.

When plants in the growth rooms were moved from conditions which had induced

complete dormancy to conditions of higher temperatures and long days without a period of low temperatures, it was shown that the original apical meristems failed to develop further and that axillary buds elongated instead. These buds arose close to soil level in that region of the shoot which has been termed the replacement zone, since in the open it is from this region that an axillary bud develops into the replacement shoot in the second, flowering year of the original shoot. The state of dormancy of buds in this region appears to differ from the dormancy induced in the apical meristem since it does not require a period of low temperature to initiate active growth. It seems probable that axillary buds are prevented from elongation by a form of induced dormancy controlled by the activity of the apical meristem. When the latter becomes dormant, this apical dominance is lost. If the plants are now moved, without a period of low temperatures, into an environment in which growth is possible, the terminal meristem is unable to resume growth and an axillary bud elongates. The behaviour of buds in the replacement zone, and the dormancy of mature raspberry shoots, will be discussed when work on flower development has been described in later papers.

SUMMARY.

Experiments in growth rooms indicate that day-length and temperature largely determine the behaviour of emergent raspberry root suckers. Short days and cool temperatures induce dormancy in these shoots, whereas long days and higher temperatures maintain the shoot in a state of vegetative elongation. When dormancy is complete, a period of low temperature is necessary before the apical meristem readily resumes growth, although new shoots may develop from axillary buds near ground level if plants experience good growing conditions before dormancy of the original shoots has been broken. The results explain the behaviour of raspberry root suckers that appear above ground in the autumn in cool temperate climates.

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EFFECTS OF ENVIRONMENT ON *RUBUS IDAEUS* L.

IV. FLOWER INITIATION AND DEVELOPMENT OF THE INFLORESCENCE

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FLOWER initiation and the development of the inflorescence of a number of varieties of raspberry have been studied both in America and Britain. These investigations have been primarily concerned with the time of flower initiation in axillary buds in relation to the season and to their position on the shoot, with the form and development of the inflorescence within the dormant bud, with the development of sub-axillary buds and with the causes of winter damage to dormant shoots. With the exception of the causes of winter damage, these studies are summarized below.

Time of flower initiation. Macdaniels (1922) found that there was no apparent differentiation in axillary buds of the varieties Cuthbert, Marlboro and Herbert growing in New York State in the open in early October and that growing points were partially differentiated early in January. Waldo (1933) stated that in Oregon, Cuthbert, Marlboro and Lloyd George had all differentiated fruit buds by November. Similarly Mathers (1952) in Scotland found that with the varieties Malling Promise, Malling Landmark and Lloyd George the bud was entirely vegetative in July and floral development was initiated in the middle of September. Wood and Robertson (1957) and Robertson (1957), also in Scotland, confirmed these results with the varieties Malling Landmark and Lloyd George and extended the work to the variety Malling Notable, in all of which flower primordia were visible on all primary inflorescences examined in September.

Flower initiation in relation to the position of the bud on the shoot. Macdaniels (1922) did not specifically study this aspect, as he concluded that all axillary buds were potentially flower buds. Waldo stated that fruit bud differentiation proceeded generally from the tip downwards in all red raspberries ; on the other hand Mathers (1952) found that, with the varieties examined by him, buds in the region of 5 to 10 below the terminal bud were always the most advanced.

Rate of development of the inflorescence. Development of the inflorescence proceeds fairly rapidly from the time of flower initiation until October or early November (Mathers, 1952 ; Robertson, 1957), followed by a period of reduced activity in December and January (Mathers, 1952), or from early December to early March (Waldo, 1933). In early spring a second period of rapid growth and development occurs before bud-break and Wood and Robertson (1957) found evidence of a renewal, or increased rate, of flower initiation during February and March.

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Secondary or sub-axillary buds. Waldo (1933) drew attention to the existence, in a number of varieties, of secondary buds outside and slightly below the main axillary bud. He also pointed out that differentiation was later in these buds and that they could act as replacement fruiting laterals when severe winter conditions damaged the primary axillary bud. The importance of this aspect was stressed by Ruxton and Modlibowska (1954) and has been studied by Wood and Robertson (1957).

Before examining the effect of controlled environmental conditions on flower initiation, a study of initiation and development in the field was carried out under the climatic conditions of the East Midlands.

Materials and methods.

Two varieties were examined, Malling Promise and Lloyd George. Shoots from a three-year-old plantation were collected at weekly intervals from July to October and at fortnightly intervals thereafter until bud-break. Every fifth axillary bud was examined from the apex of the shoot down to about three centimetres below soil level.

In addition five terminal buds were collected and examined at weekly intervals from July onwards. The behaviour of the terminal bud of the shoot was examined since the variety Lloyd George frequently develops a terminal inflorescence in the autumn of the season in which the vegetative shoot grows. Also, the time of flower initiation in both terminal and axillary buds in relation to the elongation or dormancy of the shoot was recorded.

Longitudinal sections of each bud were cut with a freezing microtome, and a series of scale drawings of the median longitudinal section was made, thus giving a clear indication of the state of the meristem.

Results.

Flower initiation in terminal buds.

In the variety Malling Promise flower initiation was first evident in four of the five terminal buds examined in the second week of September and thereafter in all terminal buds examined. Initiation occurred after elongation of the shoot had ceased. Although no distinct terminal rosette of leaves developed on mature shoots at the conclusion of the vegetative phase, there were visible differences between the appearance of the terminal regions of elongating shoots and those which had ceased elongation and were becoming dormant (Fig. 1).

Flower initiation in the terminal buds of Lloyd George occurred over a longer period. The first instance of flower initiation was found in a terminal bud in the last week of July. Thereafter an increasing number of terminal buds were found to contain flower primordia and initiation had occurred in all terminal buds examined after the third week of August. In those in which flower initiation occurred earliest the shoots still appeared to be elongating (comparable with Fig. 1, A) and it is probable that these shoots would have developed a terminal inflorescence in the same year, as did many of the shoots in the field. Terminal buds in which initiation occurred later were at the stage shown in Fig. 1, B; the shoots had ceased elongation and were becoming dormant.

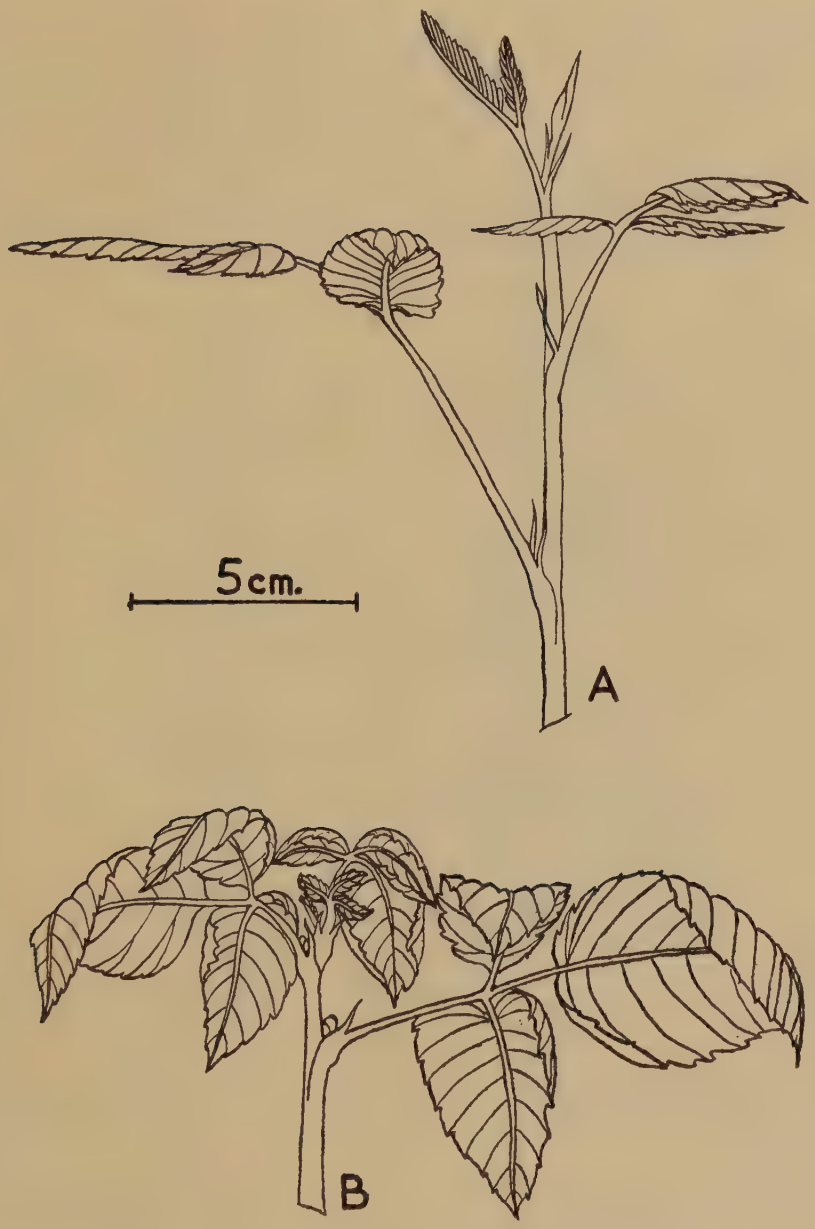

FIG. 1.

Contrast between an elongating and a dormant shoot, var. Malling Promise. A, terminal portion of a vigorously elongating shoot drawn in late May ; B, a shoot which had ceased elongation, drawn in late October. The terminal leaf cluster, the short petioles and the large axillary buds are characteristic of the latter.

Flower initiation in axillary buds.

The earliest indication of flower initiation is a broadening of the apical meristem and an elongation of the growing point. With Malling Promise flower initiation was evident in axillary buds in the second week in September, that is at the same time as in the terminal buds. With Lloyd George flower initiation was earlier, the first clear evidence in axillary buds being found in the fourth week of August. This was later than the occurrence of flower initiation in a majority of terminal buds of this variety. The apical meristematic region of the most advanced axillary bud at each sampling is shown in Fig. 2 for Malling Promise and in Fig. 3 for Lloyd George.

Flower initiation and development in relation to the position of axillary buds and to season.

With the variety Malling Promise flower initiation was first seen in axillary buds in the region of five to ten buds below the apex. Thereafter flower initiation occurred in buds progressively lower down the shoot. By early December all axillary buds except ten or twelve at lower levels contained flower primordia. No evidence of further initiation was found throughout December and early January but in late January flower primordia were found in buds towards the base of the shoot. Initiation did not occur in axillary buds at and immediately below soil level. These buds were still apparently in a vegetative state when bud-break occurred in April.

The development of the inflorescence in axillary buds in the region of the shoot where initiation was first seen was generally more advanced than in buds lower down the shoot. This lead was maintained throughout the dormant period and buds in this region of the shoot were the first to expand in the spring. In general, the inflorescence within the bud developed steadily from the time of initiation until early December. Little change took place in late December and early January, but in late January a further period of growth and development of the inflorescence was evident, buds examined at this time showing an increasing complexity as floral organs developed and more flower initials appeared.

A similar gradient of flower initiation and development was found with the variety Lloyd George. The first axillary buds in which flower primordia were found were in the region of five to fifteen below the terminal bud and initiation occurred progressively later in buds farther down the shoot. Differences in the rate of development of the inflorescence in axillary buds in different regions of the shoot were less marked than in Malling Promise. A few buds at the base of the shoot remained vegetative. Initiation and development of the apical and meristematic region in terminal and axillary buds of the variety Malling Promise in relation to position and time are shown in Fig. 4.

Form of flower initiation and development.

The terminal flower is the first to develop on the floral axis and, as the latter elongates, flower primordia arise in succession in the axils of bracts to form the terminal inflorescence within the dormant bud. Behind this terminal inflorescence meristems in the axils of leaf primordia initiate secondary inflorescences which, in turn, consist of a terminal flower with flower primordia developing behind it. This form of initiation and development within the dormant bud results in a complex

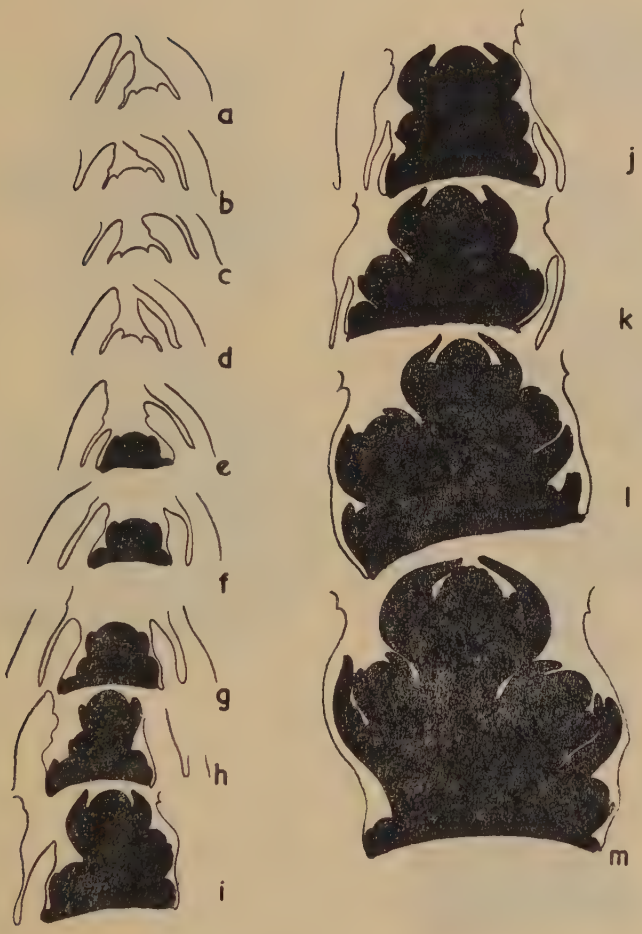

Fig. 2.

Flower initiation in Malling Promise ; form and early development shown. Each figure is a scale drawing (× 100) of the median longitudinal section of the most advanced axillary bud at each sampling. Only the apical region of the bud has been drawn. (For a section through a complete bud see Fig. 5.)

Dates when buds were examined : a, July 1956, 2nd week ; b, July, 4th week ; c, Aug., 2nd week ; d, Aug., 4th week ; e, Sept., 2nd week ; f, Sept., 4th week ; g, Oct., 2nd week ; h, Oct., 4th week ; i, Nov., 2nd week ; j, Nov., 4th week ; k, Dec., 2nd week ; l, Dec., 4th week ; m, Jan. 1957, 2nd week.

FIG. 3.

Flower initiation in Lloyd George, illustrated as in Fig. 2. It can be seen that flower initiation of axillary buds was earlier with Lloyd George than with Malling Promise.

Dates when buds were examined : a, July 1956, 4th week ; b, Aug., 2nd week ; c, Aug., 4th week ; d, Sept., 2nd week ; e, Sept., 4th week ; f, Oct., 2nd week ; g, Oct., 4th week ; h, Dec., 2nd week ; i, Jan. 1957, 2nd week.

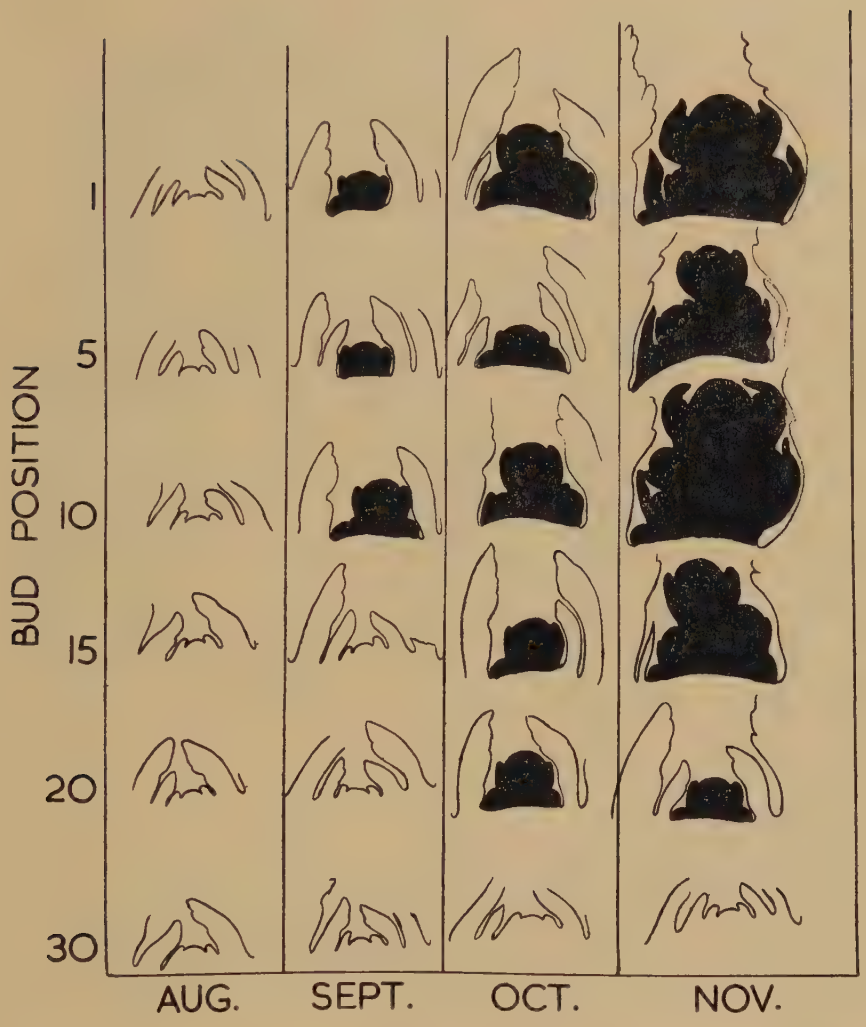

FIG. 4.

Flower initiation down the shoot, var. Malling Promise. The position of the bud is indicated by the numbers, No. 1 being the terminal bud of the shoot. The state of flower initiation and development at the middle of each month has been drawn (×100).

inflorescence comprising a terminal inflorescence and secondary inflorescences. The development of flower parts has been dealt with in detail by Mathers (1952).

In addition, with the variety Lloyd George, flower initiation and the development of an inflorescence occur in the sub-axillary buds on the shoot. A section through an axillary and sub-axillary bud of this variety is shown in Fig. 5.

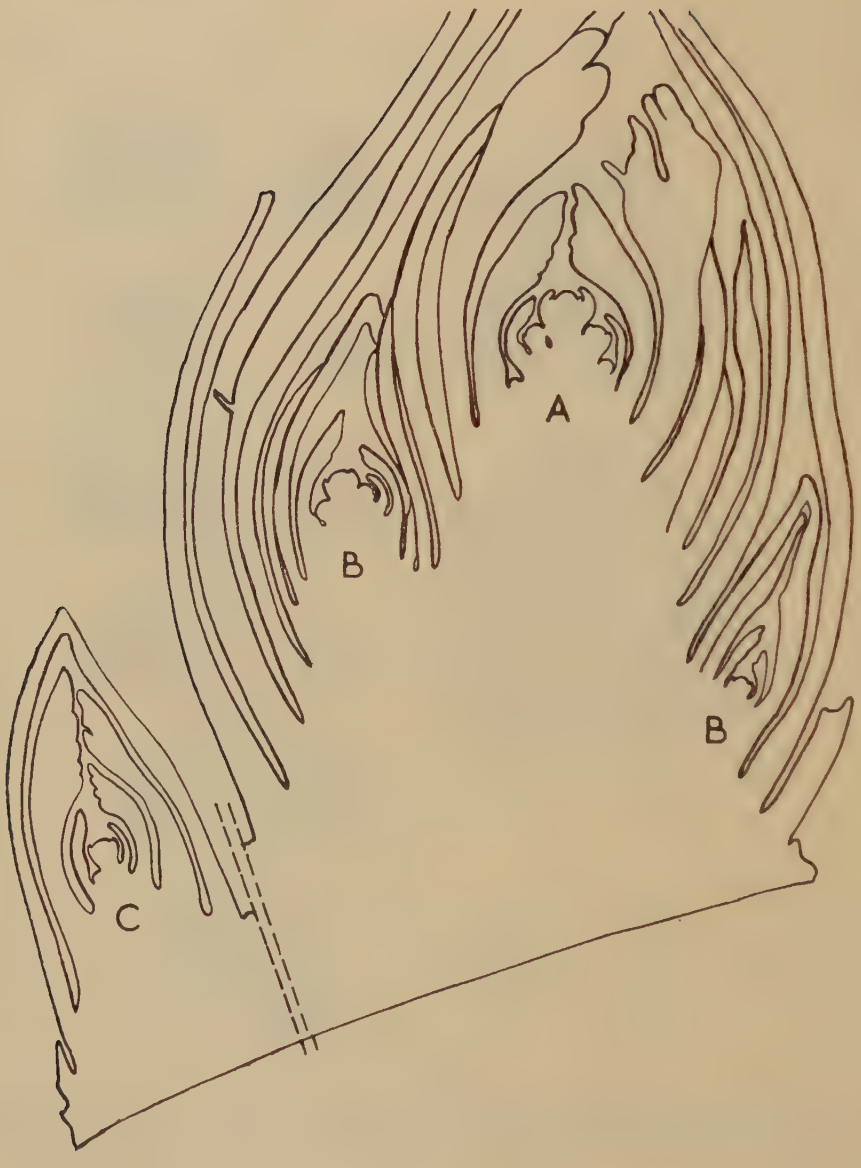

FIG. 5.

Radial longitudinal section (×50) of an entire axillary bud, var. Lloyd George.

A. Terminal inflorescence, consisting of a terminal flower with secondary flower primordia developing below it.

B. Secondary inflorescences arising in the leaf axils within the dormant axillary bud.

C. Secondary or sub-axillary bud which is a characteristic of this variety and is not found in Malling Promise.

Drawn at the end of September 1956. The bud was sectioned in two parts and the dotted lines indicate the point of junction between the two sections.

DISCUSSION.

The present investigation has shown that flower initiation in axillary buds of the varieties Lloyd George and Malling Promise occurs in early autumn. Minor differences in the time of flower initiation reported in earlier papers may well be due to differences in the climatic conditions under which the plants were growing or in the position on the shoot from which buds were removed for examination. In both varieties flower initiation occurred later in axillary buds lower down the shoot. The basal buds remained vegetative and developed into the vegetative shoots which replaced the fruiting shoot in the following year.

Workers have reported different times for the rate of development of the inflorescence within the dormant axillary bud. While this also will depend upon the position on the shoot of buds examined, it is probable that, once flower initiation has occurred, the rate of development of the inflorescence is largely governed by prevailing temperature, periods of low temperature arresting development and retarding what would otherwise be a continuous process.

The relationship between flower initiation and the onset of dormancy is of particular interest. In the previous paper (Williams, 1959) it was shown that short days and cool temperatures could bring about the dormancy of young shoots. Flower initiation, however, did not occur. In the mature shoot growing in the field, the onset of dormancy in these varieties precedes flower initiation except in some shoots of Lloyd George. Under these conditions, the latter develops a terminal inflorescence in the autumn of the same year in which the vegetative shoot is formed. It is possible that flower initiation in the meristem of the terminal bud of this variety occurs when the meristem reaches a certain physiological stage—a state of " ripeness to flower "—and is not a direct response to changes in specific environmental factors.

SUMMARY.

Work dealing with the initiation and development of flowering in varieties of *Rubus idaeus* L. is reviewed. The present investigation of the varieties Malling Promise and Lloyd George has shown that flower initiation occurs in both varieties in the autumn after shoot elongation has ceased, except for a number of terminal buds of Lloyd George. In these, flower initiation has occurred earlier, while the shoot is still elongating, and development of the terminal inflorescence is completed in the autumn of the same year.

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THE EFFECT OF THE YIELD VARIABILITY OF AMELONADO CACAO ON THE DESIGN OF FERTILIZER FIELD EXPERIMENTS IN GHANA

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It is essential that designs used in fertilizer field experiments shall be capable of detecting the responses that are expected to occur. The variability of the material to be used must be estimated so that appropriate designs can be employed. Extreme variability in the yields of perennial crops, and particularly cacao, calls for care in the choice of designs. In this paper the yield variability of Amelonado cacao growing in Ghana is investigated with a view to assessing the minimum requirements for the design of fertilizer field experiments.

In the past in Ghana, uncontrolled pests and diseases have rendered the accurate measurement of yield responses either impossible or suspect. However, in recent years adequate control measures have greatly increased the possibility of accurate field experimentation and a new phase of nutritional field experiments has begun.

As early as 1927, Auchinleck (1) in Ghana noted the large variability of the yields between trees, and also (2) that their yields were not normally distributed. They were in fact positively skew. In Trinidad in 1932, Cheesman and Pound (3) concluded that plots of 12 to 18 trees might be expected to demonstrate responses of the order of 30 per cent. at the $P=0{\cdot}05$ level of significance for experiments conducted within a single year and when 4×4 latin square designs are used. They also advocated the use of yield calibration to increase precision.

A detailed economic survey carried out in Trinidad by Shephard (13) in 1937 indicated a large percentage of poor-bearing trees in every field he examined. This suggests that a non-normal distribution of yields of single trees existed in both young and mature cacao. Jolly (7) in 1942, using plots of 0·04 to 0·33 acre, found coefficients of variability ranging from 11 to 50 per cent. in uniformity trials in Grenada, B.W.I.

Pearce and Thom (11) reported in 1951 yield variabilities from crop records of Nigerian smallholdings. They found that small plots of 0·01–0·025 acre could be used to detect a 20 per cent. difference between treatment means at a significance level of $P=0{\cdot}05$, provided that 15–25 replicates were used and that two years of pre-treatment records were available for calibration. Non-normality of yield distributions in Ghana and the possibility of applying logarithmic transformation were described by Rogers and Knight (12) in 1953.

Two facts appear common to all the studies so far made. The yields of cacao trees of all ages are extremely variable, even when grown under the most uniform conditions available, and the distribution of these yields is frequently non-normal.

Materials.

In this paper the yield records of Amelonado cacao trees grown from seed are used. This is the standard variety grown in Ghana and Nigeria and is probably more genetically uniform than other recently introduced varieties. Sufficient data for analysis are not yet available from these other varieties or from clonal material. Four classes of cacao were considered :

(*a*) Young Amelonado cacao planted in straight lines at uniform spacing and under the most uniform conditions of natural shade obtainable in the field.

Individual tree records of 6,000 trees planted as a uniformity trial at W.A.C.R.I. in 1947 were available for the period 1956 to 1958. Records from 1,600 of these trees were analysed.

(*b*) Mature cacao planted as above.

The only records suitable for analysis here were from 500 trees in the 1st Progeny Trial Area planted at W.A.C.R.I. in 1939–41. These trees comprised four Amelonado selections whose performances had been similar since planting.

(*c*) Young cacao planted at random under variable shade conditions, as typified by a good peasant farm.

The individual tree records of 1,000 trees planted at Adonkwanta in 1945 were analysed. Yield data were available for the period 1953 to 1958.

(*d*) Mature cacao (more than 20 years old) growing as in (*c*).

The yield records of 1,000 trees at each of six sites, Juaso, Mampong, Domiabra, Obuasi, Antoakrom and Brofoyedru, for the period 1954 to 1958 were used. In addition, at W.A.C.R.I., twenty 0·25 acre and twenty 0·063 acre plots, totalling approximately 2,800 and 1,000 trees respectively, have been yield-recorded since 1938. Only the period 1948 to 1958 was studied in this paper, since pest and disease control measures (against capsids, swollen shoot virus and black pod disease) were effective only during this period.

For convenience, these four classes of cacao will be referred to in this paper as Uniform-young, Uniform-mature, Random-young and Random-mature cacao. Amelonado cacao has been arbitrarily considered as mature after bearing for about ten years.

With the exception of pre-1954 yields on W.A.C.R.I. Old Station, all of the trees considered in this study were receiving capsid control. No evidence is yet available to suggest that the increased yields obtained by reducing capsid are accompanied by decreased yield variability between trees.

Methods.

Pod numbers have been used as the measure of yield performance. This method of recording is both simple and reliable.

The yield data have been considered in five stages, as follows :

(*a*) The distributions of yield data from single trees were investigated.

(*b*) Non-normal distributions were encountered and attempts were made to obtain more normal data by grouping contiguous trees without overlapping of groups, applying logarithmic transformation or a combination of both methods. The minimum grouping needed to produce a near-normal distribution was regarded as the criterion for choosing the smallest practical experimental unit. The spacing of the trees within the group will determine the area of this experimental unit.

(*c*) Coefficients of variability were calculated on normally or near-normally distributed data.

(*d*) Cunningham and Lamb (5) have demonstrated that a 45 per cent. response to fertilizers can be achieved under very good experimental conditions. Unpublished data from other trials in Ghana suggest that responses varying from 20 to 50 per cent. can be expected. The limits on design imposed in this paper are that replications used should be adequate to detect 20 per cent. responses at the $P=0{\cdot}05$ level of significance. The methods of Pearce (9), Pearce and Thom (10) and Christensen (4) were used to calculate the required replications. The formulae $N=0{\cdot}022V^2$ and $N=1375s^2$ (N, the number of replications ; V, the coefficient of variability ; s, the standard error) were applied respectively to untransformed and transformed data.

(*e*) The reduction of variability and replication by calibration and analysis of covariance were investigated.

The above methods have been used with a view to adopting randomized-block designs ; these are most suitable for field experiments in Ghana.

In plots of fixed area in random cacao, yields were always corrected for the actual number of trees per plot, tree density ranging from 400 to 1,000 trees per acre.

The possibility of using growth measurements (for example, girths) instead of pod-counts was considered, but sufficient data were not available. Unpublished data at W.A.C.R.I. and the work of Jones and Maliphant (8) in Trinidad indicate a good correlation between tree girths and subsequent yields, which might provide an alternative method for calibrating young cacao when it comes into bearing.

Practical considerations.

The shallow lateral root system of mature cacao trees can extend 15 ft. or more from the trunk. In nutritional experiments a guard space of at least 15 ft. is therefore essential.

In Ghana, 8 ft.×8 ft. spacing of uniform cacao is regarded as optimal for the yield per acre from Amelonado trees (14). This necessitates double guard rows between plots and limits considerably the proportion of experimental trees. Table I illustrates that small plots do not use trees economically ; sixteen or more trees per plot seem preferable.

TABLE I.

Effect of plot-size on utilization of available trees in uniformly spaced cacao.

Nos. of trees per plot*	Percentage of available trees	
	Experimental	Guard (double rows)
1	11	89
4 (2×2)	25	75
9 (3×3)	36	64
16 (4×4)	44	56
25 (5×5)	51	49
36 (6×6)	56	44
100 (10×10)	69	31

* Square plots are more efficient than other rectangular plots.

Randomly planted cacao presents additional practical problems. Plots must be identified with permanent markers able to withstand the rigours of a tropical climate for several seasons. Great inconvenience, and even the abandonment of an experiment, can result from the loss of any of these markers. Guard areas rather than guard rows must be used between plots.

At W.A.C.R.I., Arnold* and Cunningham introduced a circular plot technique which provides approximately 50 per cent. of experimental trees and avoids the use of permanent artificial markers. The central tree in each plot, called the " key-tree ", is identified by three broad red bands painted on its trunk. Eight temporary pegs are placed $22\frac{1}{2}$ ft. from the key-tree, marking out a circular plot of 0·037 acre. Only trees 3 ft. or more within the circumference of the plot are considered experimental. The actual number of experimental trees varied from 12 to 25 per plot according to the density of planting. Location of the key-tree, positioning the pegs, application of fertilizer and final removal of the pegs takes two men about ten minutes per plot. Adequate guard areas are provided by ensuring that the nearest points on the circumferences of neighbouring plots are at least 6 ft. to 8 ft. apart. Only the marked key-trees are left at the site to identify the plots. This technique has been successfully employed, especially at isolated sites.

Results.

(*a*) *Uniform-young cacao.*

The yield distribution of single trees was not normal. Groups of 4, 9, 16, 25 and 100 trees showed that increasing group size was accompanied by a tendency towards a normal distribution (Fig. 1). Although only 100-tree groups gave near-normal distributions, smaller groups (e.g. of 16 trees) gave a near-normal distribution when the plot yields were transformed by logarithms (Fig. 2). This suggests that a 16-tree unit would be satisfactory. With cacao spaced at 8 ft.×8 ft. the unit area required would be 0·024 acre without guard rows and 0·053 acre with double guard rows.

The number of replications needed is shown in Table IV. The areas of cacao required per treatment were calculated from the product of replication and plot area.

Yield data for this class of cacao were insufficient to attempt calibration. Pre-bearing girth data were considered as an alternative to yields for calibration but were not available.

(*b*) *Uniform-mature cacao.*

Very skew distributions of yield of single trees and small groups still occurred. However, Table II shows that after 18 years the distribution of the yields from 16-tree groups became reasonably normal. A convenient plot size and population at 8 ft.×8 ft. spacing would be the same as for Uniform-young cacao, but transformation of yields is no longer necessary.

It was not possible to form compact 16-tree groups of the four Amelonado selections used in this class because of the original layout of this Progeny Trial, but trees sited as close to each other as possible were used. Table IV shows the great

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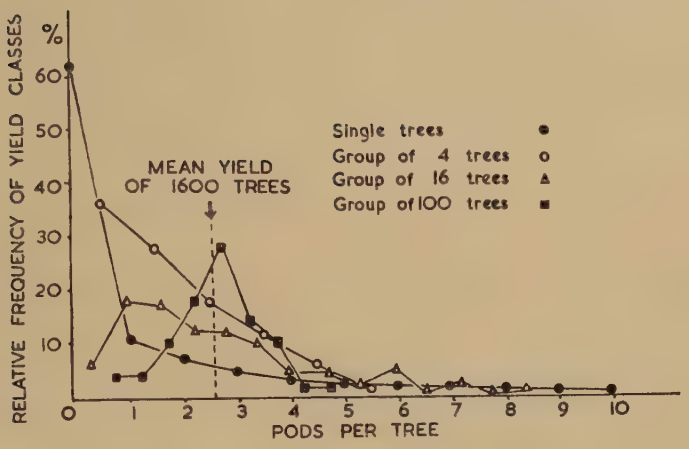

FIG. 1.

Relation between relative frequency of yields when 1,600 trees (Uniform-young, W.A.C.R.I., season 1956–7) were considered singly or as groups of 4, 16, and 100 trees. Group yields are expressed in pods per tree to make the different groupings graphically comparable. Frequency distributions of 9- and 25-tree groups omitted from diagram for clarity, as they fell in the correct sequence. The mean yield of the 1,600 trees was 2·54 pods per tree (shown by broken line); single tree yields ranged from 0 to 37 pods per tree.

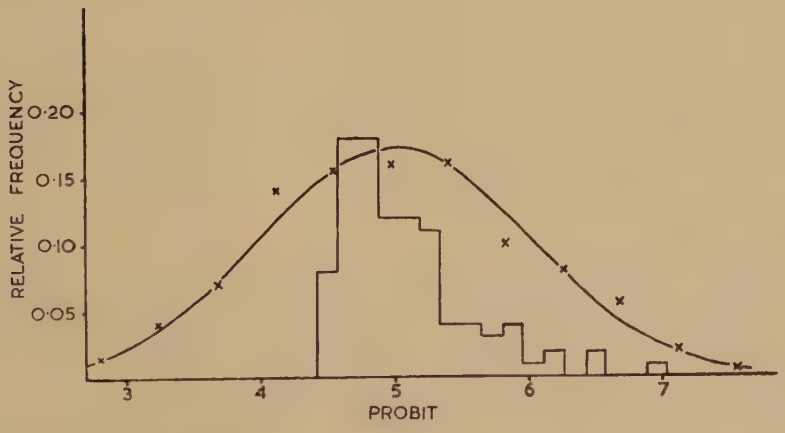

FIG. 2.

Effect of logarithmic transformation on the distribution of yields of groups of 16 trees of Uniform-young cacao (the same 1,600 trees as in Fig. 1). The points plotted are means between adjacent yield classes.

TABLE II.

Yield distribution of 16-tree groups of uniform-mature cacao.

Yield interval (pods per tree)	0–4·9	5–9·9	10–14·9	15–19·9	20–24·9	25–29·9	30–34·9
10 years old ..	9	12	5	4	2	0	0
14 years old ..	4	13	8	3	3	1	0
18 years old ..	1	9	8	9	3	2	0

variability of these groups and the large replication needed for single-season experiments.

Seasonal yield correlations are shown in Table III. It is apparent that the correlation between single seasons can be unreliable for all the classes of cacao studied, whereas the correlation between period seasons was satisfactory in all cases tested.

The yields of this Uniform-mature cacao were not recorded between 1954 and 1957 and adjustment of the latest years' yields was not possible. However, adjustment reduced the variability of the paired seasons 1952 and 1953 to 25 per cent. (Table IV). It seems reasonable to assume that the lower variability in 1957 could have been adjusted to a level even lower than 25 per cent.

(*c*) *Random-young cacao.*

The distribution of yields was not normal for groups of 12–25 trees contained in circular plots of 0·037 acre (see *Practical considerations*, para. 4) even with logarithmic transformation. Pairing seasons improved distributions but replication after adjustment remained impracticably high (Table IV).

When a randomized-block design was not used, a unit consisted of 3 randomly selected circular plots (total area 0·11 acre) rather than a single circular plot. Transformation within a season or pairing seasons gave normal distributions for the yield from such complex units. For single seasons the necessary replication was very high, but for paired seasons after adjustment it was low (Table IV).

(*d*) *Random-mature cacao.*

At all sites examined, the distribution of yields from single trees and very small groups was not normal, both with and without transformation. Circular plots of 0·037 acre (12 to 25 trees), square plots of 0·063 acre (45 to 60 trees) and 0·25 acre (100 to 150 trees) gave near-normal distributions without transformation, indicating that plot sizes of 0·037 acre and greater are satisfactory.

The coefficients of variability within single seasons ranged from 30 to 60 per cent., with a slight decrease of variability with increase in plot size. The W.A.C.R.I. Old Station records showed no decrease of variability with age over the ten-year period 1948 to 1958. Table IV shows that adjustment of paired seasons considerably reduced the variability and the replications required. Plots of 0·037 acre and 0·063 acre needed less area per treatment than the 0·25 acre plots whose advantage of lower variability was offset by their greater size.

Table III.

Seasonal yield correlation.

Class of Amelonado cacao	Site	No. of plots	No. of trees per plot	Plot size in acres	Single season correlation coefficients									Paired seasons correlation coefficients †						
					1948–49 and 1949–50	1949–50 and 1950–51	1950–51 and 1951–52	1951–52 and 1952–53	1952–53 and 1953–54	1953–54 and 1954–55	1954–55 and 1955–56	1955–56 and 1956–57	1956–57 and 1957–58	1948–49 + 1949–50 and 1950–51 + 1951–52	1949–50 + 1950–51 and 1951–52 + 1952–53	1950–51 + 1951–52 and 1952–53 + 1953–54	1951–52 + 1952–53 and 1953–54 + 1954–55	1952–53 + 1953–54 and 1954–55 + 1955–56	1953–54 + 1954–55 and 1955–56 + 1956–57	1954–55 + 1955–56 and 1956–57 + 1957–58
Uniform-young	W.A.C.R.I. Block G	48	16	0·024	—	—	—	—	—	—	—	—	** 0·42	—	—	—	—	—	—	—
Uniform-mature	W.A.C.R.I. 1st P.T.A.	15	16	0·024	—	*** 0·92	*** 0·78	*** 0·86	*** 0·50	—	—	—	—	—	—	*** 0·89	—	—	—	—
Random-young	Adon-kwanta	9‡ groups	40–60	0·11	—	—	—	—	—	—	*** 0·83	*** 0·91	0·30	—	—	—	—	—	—	*** 0·79
Random-mature	W.A.C.R.I. Old Station	20	100–150	0·25	*** 0·87	*** 0·94	** 0·61	** 0·66	*** 0·92	*** 0·92	*** 0·94	*** 0·93	*** 0·91	*** 0·83	*** 0·82	*** 0·83	*** 0·75	—	—	—
Random-mature	W.A.C.R.I. Old Station	20	45–60	0·063	** 0·65	*** 0·78	*** 0·76	*** 0·83	* 0·51	0·33	* 0·55	** 0·60	* 0·47	—	—	—	—	—	—	*** 0·80
Random-mature	Antoakrom	32	12–25	0·037	—	—	—	—	—	—	*** 0·76	*** 0·65	*** 0·67	—	—	—	—	—	—	*** 0·83

† The correlation coefficients for two-year periods were calculated only when those for one-year periods were unsatisfactory.
‡ See results Sec. C, para. 2 for method of grouping.
Asterisks indicate levels of significance.

DISCUSSION.

In Ghana, areas normally available for fertilizer field experiments range in size from 1 to 5 acres. In view of this, it can be seen from Table IV that, for all classes of cacao, experiments within a single season are either impossible or must be very simple. However, when paired season adjustments are made, the scope of experiments is widened. For example, single season experiments with 0·063 acre plots of Random-mature cacao required approximately 2 acres per treatment but, with paired season adjustment, the required area decreased to 0·69 acre per treatment. This increases the number of treatments which can be applied on a 5-acre site from 2 to 7.

It would appear from a consideration of the data presented in Tables III and IV that accurate and reliable fertilizer field experiments can be conducted in Ghana only on the following basis :

(1) Plots of at least 16 trees must be used in uniformly spaced cacao ; at an 8 ft. × 8 ft. spacing these plots cover an area of 0·024 acre and require 0·053 acre with their associated guard rows. Plots of at least 12 to 25 trees are needed in randomly planted cacao ; circular plots of 0·037 acre contain this range of trees and require 0·074 acre with associated guard areas.

(2) The yields of small plots of young cacao must be transformed logarithmically in order to obtain near-normally distributed plot yields.

(3) Satisfactory reduction in variability, decrease in required replication and increase in precision are obtained by calibration and adjustment. Single season calibration was unsatisfactory : adjustment of paired seasons by paired seasons must be carried out, and any experiment will therefore cover four seasons.

(4) A replication of about 12 is required if a 20 per cent. difference between treatment means is to be shown significant at the $P=0·05$ level. When 16-tree plots are used, nearly 1 acre is needed per treatment.

The preceding points all emphasize the recommendations of Hoblyn (6) that, at this stage of cacao field experimentation, simplicity must be the keynote of design. They also suggest that many of the past and current field experiments in Ghana are incapable of detecting responses of less than 50 per cent. Inadequate designs provide one possible explanation of the conflicting and disappointing results of fertilizer experiments, not only in Ghana, but in other cacao-growing areas of the world. There is little evidence to show that cacao yields in other territories and with other varieties, with the possible exception of clones, are any less variable than the cacao yields studied in this paper.

Although this investigation has been primarily concerned with the design of nutritional field experiments, it is possible that the results obtained here may be applied to other cultural experiments.

SUMMARY.

Yields of Amelonado cacao grown in Ghana have been analysed in an attempt to assess the minimum requirements for the design of fertilizer field experiments capable of detecting 20 per cent. yield responses at the $P=0·05$ level of significance. Normal distributions of yield data were obtained by grouping trees, by logarithmic transformation or by a combination of both methods. For single season experiments, coefficients of variability in the range 30 to 60 per cent. made replications too high to

Table IV.

Reduction of variability by adjustment of paired seasons.

Class of Amelonado cacao	Site	No. of plots	No. of trees per plot	Plot size in acres†	Single season				Pairs of seasons adjusted by previous pairs of seasons			
					Season	V (%)	N	A in acres	Season	V (%)	N	A in acres
Uniform-young	W.A.C.R.I. Block G	48	16	0·024 (0·053)	1956–57 1957–58	— —	97* 34*	5·14 1·80	—	—	—	—
Uniform-mature	W.A.C.R.I. 1st P.T.A.	15	16	0·024 (0·053)	1950–51 1951–52	51 48	58 51	3·07 2·70	1952–53 + 1953–54 by	25	14	0·74
					1952–53	57	72	3·82	1950–51 +			
					1953–54 1957–58	55 32	67 23	3·55 1·22	1951–52	—	—	—
Random-young	Adonkwanta	27	12–25	0·037 (0·074)	1954–55 1955–56 1956–57 1957–58	Not calculated : distribution not normal either on transformed or on untransformed data			1956–57 + 1957–58 by 1954–55 + 1955–56	35	27	2·00
		9	40–60	0·11‡ (0·22)	1954–55 1955–56	— —	38* 34*	8·36 7·48	1956–57 + 1957–58 by	9	2	0·44
					1956–57 1957–58	— —	33* 5*	7·26 1·10	1954–55 + 1955–56			
Random-mature	W.A.C.R.I. Old Station	20	100–150	0·25 (No guard areas)	1948–49 1949–50	33 33	24 24	6·00 6·00	1950–51 + 1951–52 by	18	8	2·00
					1950–51 1951–52	33 36	24 29	6·00 7·25	1948–49 + 1949–50			
Random-mature	W.A.C.R.I. Old Station	20	45–60	0·063 (No guard areas)	1953–54 1954–55	35 40	27 36	1·70 2·27	1955–56 + 1956–57 by	22	11	0·69
					1955–56 1956–57	37 37	31 31	1·95 1·95	1953–54 + 1954–55			
Random-mature	Adonkwanta	32	12–25	0·037 (0·074)	1954–55 1955–56	57 51	72 58	5·33 4·29	1956–57 + 1957–58 by	24	13	0·96
					1956–57 1957–58	48 47	51 49	3·77 3·63	1954–55 + 1955–56			

V, Coefficient of variability.
N, No. of replicates required to detect differences of 20% of the mean at P=0·05 level.
A, Area required for each treatment including associated guard rows or areas. It is assumed that double guard rows are used between plots in Uniform cacao and that in Random cacao 50% of the area is used for guarding.
*, Calculated from logarithmically transformed data.
†, The first area is for experimental trees only; the area in brackets is for experimental+guard trees. For Uniform cacao 8 ft. × 8 ft. spacing is assumed and in Random cacao circular plots of radius 22·5 ft. are used, except at W.A.C.R.I. Old Station.
‡, For technique to make data normal, see Results Section *c*, paragraph 2. This method of grouping precludes randomized block or latin square designs and has therefore not been applied to other classes of cacao.

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be practicable. Adjusting data from paired seasons reduced replication to about 12, which was just sufficiently low to make accurate experiments possible. A circular plot technique for use in random cacao is described.

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THE CONTROL OF MAGNESIUM DEFICIENCY IN DWARF PYRAMID APPLES

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The leaf symptoms of magnesium deficiency (Wallace, 1951) occur widely in apple orchards. The development of interveinal leaf scorch or necrosis, more or less characteristic but varying somewhat with the variety, and the ensuing early defoliation towards the base of the new shoots, are frequently associated with no obvious reduction in growth. The question arises, therefore, whether the appearance of such symptoms should in itself concern the fruit grower.

The necrosis of a few leaves may well indicate an unsatisfactory tree condition and in general, since leaves that become necrotic and fall early cannot be as efficient as leaves that remain green, the whole tree may benefit if by any control measures the disorder can be prevented. However, the only real test of a control measure is not its efficiency in maintaining green foliage but its effect on the growth and cropping of the tree.

It is well established that the use of Epsom salt sprays can increase the magnesium content of leaves of deficient apple trees and prevent the appearance of leaf symptoms. Growth has been shown to be increased by this treatment on apple rootstock stoolbeds at East Malling (Ford, 1958), and several workers have commented on the effects of Epsom salt sprays on various aspects of growth and fruiting in apple orchards (Chucka *et al.*, 1945 ; Wallace, 1948 ; Bould and Tolhurst, 1949 ; Woodbridge, 1955). Very little attention has, however, been paid to the assessment of the total crop response of magnesium-deficient apple trees to sprays of Epsom salt.

There is evidence that nitrogen may palliate to some extent a deficiency of magnesium (Wallace, 1953). Hoblyn (1941) reported that interveinal scorch on apple trees was reduced by sulphate of ammonia, and in America nitrogen applications have been shown to increase the magnesium content of apple leaves (Boynton and Compton, 1944 ; Cain, 1953a). Such observations suggest that urea sprays, already established as an effective means of supplying nitrogen to apple trees, might control magnesium deficiency in the orchard.

An experiment was therefore carried out at East Malling over the five seasons 1954 to 1958 to investigate the effects of sprays of Epsom salt and of urea on the growth and cropping of apple trees showing severe visual symptoms of magnesium deficiency.

Material and methods.

The trees used, dwarf pyramid Edward VII on M.VII, had shown the typical symptoms, viz. leaf necrosis and premature defoliation, for three years prior to the start of the experiment, while the magnesium content of affected leaves was low ; however, the growth was not regarded as unsatisfactory. The trees had been planted in 1949/50 at 8 ft.$\times$4 ft. on a fine sandy loam soil (Barming Series) and summer-pruned ; the alleys had been grassed down since 1952.

The successful culture of dwarf pyramid trees involves the restriction of growth by summer pruning. After the experiment started this was somewhat modified, the branch leaders being allowed to remain unpruned each season until the winter to facilitate the sampling of leaves for chemical analysis and the recording of extension growth ; lateral growths were, however, summer-pruned each year.

The sward was allowed to encroach on to the tree rows from 1956 onwards. The manurial programme consisted of 3 cwt. of sulphate of ammonia and 1 cwt. of muriate of potash per acre in each of the years 1950–55 inclusive, with an extra 1 cwt. per acre of muriate of potash in 1952, followed in 1956–58 by 4 cwt. per acre each year of a compound inorganic fertilizer containing 16 per cent. N, 16 per cent. K_2O and no phosphate. Routine sprays were applied for the control of pests and diseases.

Experimental design.

The three treatments were applied to adjacent single trees, 4 ft. apart, in each of eight randomized blocks, selected from twenty possible blocks in the row, on the basis of the relatively uniform occurrence within each block in October 1953 of comparable shoots from which preliminary leaf samples were taken. A fourth treatment, as described below, was applied on five additional trees occurring between the blocks ; the data obtained on these trees were not included in the statistical treatment of results.

Treatments.

The spray treatments in the main experiment were

(*a*) 2 per cent. Epsom salt ($MgSO_4.7H_2O$)

(*b*) 0·5 per cent. urea

and (*c*) water (control)

with the addition in each case of 0·01 per cent. Aerosol OT, which in our experience gives adequate wetting.

The treatments were applied five times during each of the seasons 1954–58 inclusive, commencing at the petal-fall stage and then as nearly as possible at 14-day intervals. Owing to seasonal variation, the dates of the first application ranged between 17th and 31st May and those of the final application correspondingly between 11th and 26th July.

A knapsack sprayer was used, a screen being placed round each tree to prevent drift. Spraying was normally carried out during the morning and sufficient material was applied to wet all the leaves thoroughly. The rate was estimated to be about 250 gallons per acre.

The five additional trees were used to test the effectiveness of low volume applications of Epsom salt. A 28 per cent. Epsom salt ($MgSO_4.7H_2O$) solution was applied in an atomized form at the rate of 3–4 gallons per acre by means of a paint spray gun, at the same time as the other sprays. In 1958 the concentration was increased to 92 per cent. Epsom salt (9·2 lb. $MgSO_4.7H_2O$ per gallon of water). This was actually achieved, despite the lower concentration given in the standard solubility tables.

Records and sampling.

Leaf symptoms. In August or September visual category records were made of the leaf colour ; at the same time the proportion of leaves showing interveinal

scorch was estimated—in 1954 for the tree as a whole and in subsequent years for spur and extension shoot leaves separately. The amount of defoliation of the leaders was similarly estimated in categories in September or October.

Growth. Annual trunk girth measurements were made during each dormant season. The girth at the end of 1953 served as an independent variate for the adjustment of subsequent growth and cropping data to allow for variability in tree size at the start of the experiment. The total increase in length of the leaders during each season was also measured, but summer-pruning the laterals precluded the possibility of estimating the total extension growth. Nevertheless, the summer prunings were measured in 1957 and 1958 as an estimate of the growth of the laterals.

Fruit bud and blossoming. The numbers of fruit buds were counted each spring and the amount and stage of blossoming were estimated visually.

Cropping. The apples from each tree were counted and weighed. Fruit colour and skin blemishes were recorded in categories.

Mineral composition of leaves. Magnesium, nitrogen and potassium were determined, as per cent. dry weight, on leaf samples taken twice each year, except for 1958 ; a sample consisted of one leaf from each of eight shoots, taken from a definite position on the shoot. The first samples were taken in July (August in 1955), when the deficiency symptoms were developing ; in 1954 and 1956 four of the five sprays had been applied, but in 1955 and 1957 all spraying had been completed at the time of this sampling. The second sampling occasion was in October (September in 1956), when symptoms were very well developed, 2–3 months after the season's spray applications ceased.

In 1954 the July samples were of the youngest fully expanded (F) leaves and of leaves at the base (B) of extension shoots, and in October of that year the apical (A) and middle (M) positions were selected. Subsequently the middle leaves (M) of extension shoots and leaves from vegetative spurs (R) were selected on each occasion.

The leaves were cleaned, dried at 80° C. after removal of midrib and petiole, and analysed by the following methods : magnesium by the Titan Yellow reagent, nitrogen by semi-micro Kjeldahl and potassium by flame photometer.

Soil analysis. In December 1956 a sample of four cores representative of the soil in the tree row within each block was taken from each of the depths 0–6, 6–12, 12–18 and 18–24 inches. These samples were air-dried, and subsequent determinations were made of pH (by glass electrode) and of the magnesium, potassium and phosphorus extracted by Morgan's reagent (1937).

RESULTS.

Leaf symptoms.

On the control trees the usual interveinal scorch symptoms first appeared between 12th and 26th July, became progressively more severe during the following weeks, and were followed by premature abscission of the affected leaves. The urea sprays were quite ineffective in preventing interveinal scorch symptoms or defoliation of the shoots.

Interveinal scorch was greatly reduced by the Epsom salt sprays, although some necrosis began to appear two to four weeks after the final application in each season. The amounts of interveinal scorch and defoliation were slight in comparison with the controls, as was clearly shown each year by the category records, of which the results for 1957 (Table I) are typical.

TABLE I.

Effect of sprays on interveinal scorch and leader defoliation.

	Date	Control	Urea	Epsom salt
Interveinal scorch on leaders ..	7th Aug. 1957	4·6	4·3	0·6
,, ,, spurs ..	,,	4·1	3·8	0·1
Defoliation on leaders	10th Oct. 1957	4·0	3·6	0·9

Category values : No leaves affected .. 0
1–10 % ,, ,, .. 1
91–100% ,, ,, .. 10

Interveinal scorch was also observed as early as 7th June in 1956 and 28th May in 1957 and 1958 on the small primary leaves of fruit spurs, and many of these leaves subsequently abscissed. The secondary spur leaves showed no symptoms at these dates but developed scorch in July on the control and urea-sprayed trees. On the trees sprayed with Epsom salt the primary leaves developed no symptoms and many of them persisted throughout the season.

Leaves were a darker green in 1954 as a result of spraying with urea, but in subsequent years the colour of the foliage appeared to be equally good on trees of all treatments.

No visible injury to the leaves resulted from any of the spray treatments, even when the 28 per cent. $MgSO_4.7H_2O$ atomized spray applied to the five additional trees was increased in concentration to a 92 per cent. solution. This treatment was less effective than the high volume application of Epsom salt in reducing the magnesium deficiency symptoms. The higher concentration used in 1958 appeared to be more effective than the 28 per cent. solution used previously.

Growth.

Trunk girth increase. An analysis of covariance of the total increase in trunk girth over the five-year period on the initial girth showed that there was no significant effect of treatments (Table II). The higher value for the Epsom salt treatment was almost entirely due to differences in the one season 1956, and indeed a separate analysis of the increment for that year in the logarithm of the girth showed that Epsom salt sprays resulted in a significantly greater relative trunk girth increase in 1956 than the other treatments (Table II).

Extension growth. As was to be expected from the method of pruning, the leader growth showed great variation. No clear differences emerged between treatments (Table II) over the total period or in any of the years (the first four seasons' data were considered in two-year periods) even when corrected for initial trunk girth. Compared with the other treatments, it is possible that the trees sprayed with Epsom salt made more extension growth in the later seasons, but the measurements of leader growth and of summer prunings were both too variable to demonstrate clearly such an effect.

Fruit bud and blossoming.

The total numbers of fruit buds per tree during the five years, after correcting for initial tree size, were 910, 912 and 891 for the control, urea and Epsom salt

Table II.

Effect of sprays on growth.

	Seasons	Control	Urea	Epsom salt	Sig. diff. (P=0·05)
*Increment in trunk girth (cm.) ..	1954–58 incl.	4·55	4·56	4·93	0·64 (min.)
Increment in logarithm of girth ..	1956	0·026	0·030	0·038	0·007
*Total leader growth (cm.)	1954+1955	954	955	803	338 (min.)
* ,, ,, ,, ,, ...	1956+1957	618	593	720	240 (min.)
* ,, ,, ,, ,, ...	1958	416	437	539	150 (min.)
* ,, ,, ,, ,, ...	1954–58 incl.	1,988	1,985	2,062	519 (min.)
*Summer prunings (cm.)	1957+1958	458	500	679	319 (min.)

* Corrected for trunk girth at end of 1953.

treatments respectively. Neither treatment differed significantly from the control, the minimum significant difference (P=0·05) being 89. Similarly no differences were shown by the records of amount and stage of blossoming.

Cropping.

The Epsom salt treatment significantly increased both the number and the weight of fruit in 1955, 1956 and 1958 (Table III), while the differences in the other seasons, although non-significant, were in the same direction. The increase in total crop over the five seasons, due to Epsom salt spraying, was very definite.

Urea spraying did increase both number and weight of fruit in 1954 but, though similar differences appeared subsequently, they did not reach significance. Over the whole period there appeared to be a real difference in number of fruits though not in weight, the fruit showing a slight tendency to be smaller, as shown by the average weight of 100 fruits.

Table III.

Effect of sprays on cropping (per tree).

Season	Weight in lb.				Number of fruits			
	Control	Urea	Epsom salt	Sig. diff. (P=0·05)	Control	Urea	Epsom salt	Sig. diff. (P=0·05)
1954	6·4	8·8*	7·8	1·8	18·4	26·9*	22·0	4·1
1955	7·6	9·5	12·1*	3·6	23·6	31·6	37·0*	11·1
1956	3·4	5·2	7·4**	2·6	10·0	15·8	18·9*	7·7
1957	7·1	8·7	9·8	4·4	19·4	23·3	24·9	10·7
1958	5·9	7·4	20·2***	4·0	19·1	25·6	59·9***	12·9
Total corrected for trunk girth at end of 1953	32·5	39·5	55·3***	9·2 (min.)	95·7	123·0*	157·5***	24·8 (min.)

*=significantly greater than control at P=0·05
**= ,, ,, ,, ,, P=0·01
***= ,, ,, ,, ,, P=0·001

The main differences in crop arising from the treatments were evidently due to the increased numbers rather than to fruit size. Since there was no effect on number of fruit buds, there were important differences in the ratio of fruits to fruit buds, expressed in Table IV as fruits harvested per 100 fruit buds. Compared with the control trees, significant effects on this ratio were obtained only for Epsom salt spraying in 1956 and 1958 and for the 5-year totals, but the general tendency for both urea and Epsom salt to increase the ratio is evident throughout. In the absence of fruitlet counts early in the season, it cannot be stated whether this was due to effects on setting or to the differential retention of fruits between setting and harvesting.

TABLE IV.

Effect of sprays on number of fruits harvested per 100 fruit buds.

Season	Control	Urea	Epsom salt	Sig. diff. (P=0·05)
1954	45·9	58·2	48·5	14·6
1955	21·4	29·3	35·9	16·1
1956	6·1	7·6	10·7*	3·8
1957	9·2	10·2	10·9	4·9
1958	7·0	9·1	19·7***	4·0
Total 1954–58 incl.	10·8	13·8	18·2***	3·8

*, ***=significantly greater than control at P=0·05 and 0·001 respectively.

Some of the fruits developed a red colour, particularly on the exposed side ; this appeared in some seasons, including 1954, to be less prevalent on the urea-sprayed trees than on the remainder. There seemed to be less russeting at the stalk end of the fruits on trees sprayed with Epsom salt than on the others.

Records on the five additional trees suggested that the response in growth and cropping to the low volume atomized sprays of Epsom salt was inferior to that of the trees sprayed with 2 per cent. Epsom salt at high volume.

Mineral composition of leaves.

Statistical analyses were carried out separately for the magnesium, nitrogen and potassium contents as percentages of the dry matter in each of the four leaf samples taken each year. Data illustrative of the principal effects are presented in Table V.

Magnesium. Throughout the four years the Epsom salt sprays significantly increased the magnesium content of all leaf samples taken in July, the effect being especially marked in the basal (B) leaves in 1954 and in the spur (R) leaves in subsequent years. Although the concentrations were lower at the time of the second sampling each season, the difference due to the Epsom salt treatment was invariably in the same direction and significant except for the A (apical) position in 1954 and the M position in 1955 and 1956.

There was no indication of any real effect of urea spraying on the magnesium status of the leaves, with the single exception of a small increase in the R position in September 1956.

The low volume Epsom salt sprays appeared less effective than the high volume sprays in raising the magnesium content of the leaves in July or maintaining the level higher in October.

TABLE V.

Effect of sprays on mineral content of leaves, as percentage of dry weight.

Element	Position (see text)	Date	Control	Urea	Epsom salt	Sig. diff. (P=0·05)
Magnesium	B	July 1954	0·16	0·15	0·34***	0·039
	R	July 1956	0·17	0·19	0·28***	0·024
	,,	Sept. 1956	0·12	0·15*	0·26***	0·024
	M	July 1957	0·16	0·15	0·25***	0·021
	,,	Oct. 1957	0·10	0·11	0·18***	0·027
Nitrogen	F	July 1954	2·55	2·90***	2·50	0·221
	B	July 1954	2·30	2·52*	2·21	0·179
	R	July 1956	2·46	2·60	2·54	0·151
	,,	Sept. 1956	2·23	2·28	2·34*	0·072
	M	July 1957	2·71	2·76	2·61	0·225
	,,	Oct. 1957	2·36	2·41	2·29	0·168
Potassium	B	July 1954	1·71	1·50	1·31*	0·267
	R	July 1956	1·46	1·31	1·45	0·221
	,,	Sept. 1956	1·77	1·63*	1·77	0·122
	M	July 1957	1·75	1·65	1·72	0·188
	,,	Oct. 1957	1·71	1·69	2·01*	0·252
	R	Oct. 1957	1·32	1·25	1·66***	0·167

*, **, ***, see Table III.

Other analyses confirmed that the development of interveinal necrosis on the primary spur leaves of control trees in June 1956 was associated with low magnesium content.

Nitrogen. There was a general tendency for urea to increase the nitrogen content of the leaves, particularly at the earlier sampling each year. This effect was significant only in the first season, when there was a marked increase in both F (youngest fully expanded leaves) and B positions in July.

There is also a suggestion of a general depressant effect of Epsom salt spraying on leaf nitrogen content, but the concentration in the leaves was significantly lower than that of the controls only in the A position sample of October 1954. The 1956 season appeared exceptional, for the nitrogen content of spur (R) leaves of the Epsom salt treatment appeared higher than that of the controls in both July and September.

Potassium. At first there appeared to be a general tendency for Epsom salt sprays to reduce the potassium concentration in the leaves, although this effect was significant only in the basal (B) leaves of July 1954. Later there was a trend towards a higher level of potassium in the middle (M) leaves in October; this attained significance at P=0·05 in October 1957, and at the same time the potassium concentration in the spur (R) leaves was also markedly increased (P=0·001) by the Epsom salt treatment.

The treatment means indicate that urea sprays probably slightly but consistently reduced the potassium content of the leaves.

Soil analysis.

The levels of both "available" potassium and "available" magnesium, as indicated by the concentration in the extract (Table VI), were considered to be rather

low for apple growing, but the K/Mg ratio was not higher than the values common in fruit-growing soils. The pH data showed the soil to be slightly alkaline below the top 6 inches.

TABLE VI.

Analysis of soil sampled in December 1956 ; mean of all blocks.

Depth	pH	Phosphorus*	Potassium*	Magnesium*	K/Mg ratio
0–6 in.	6·95	5·2	34·6	25·0	1·40
6–12 ,,	7·64	3·2	20·5	15·8	1·33
12–18 ,,	7·49	0·8	15·6	11·8	1·38
18–24 ,,	7·44	0·5	12·5	13·0	1·08

* Parts per million of the element *in the extract* (one part of air-dry soil to two parts of Morgan's reagent, shaking time 2 min.).

DISCUSSION.

This trial has confirmed the effect of Epsom salt sprays in raising the magnesium status of leaves of apple trees on which symptoms of magnesium deficiency had been observed, and thereby delaying the development and reducing the severity of leaf symptoms and the subsequent defoliation of shoots. The study has also shown that, in this susceptible combination of variety and rootstock (Edward VII apple on M.VII), magnesium deficiency symptoms can develop on certain leaves much earlier in the season than has generally been reported. Similar early-season leaf symptoms were found in America by Moon *et al.* (1952). It is not possible at present to conclude whether the absence of such symptoms on the trees sprayed with Epsom salt was due to the effect of the one spray that had been applied at petal-fall or to a residual effect of the previous season's spraying.

Despite the severity of the leaf symptoms on the trees before the experiment started, their growth was not unsatisfactory, and indeed, except in the trunk girth increase during the third year of the trial, no clear effects of Epsom salt spraying on growth were obtained ; further, the number of fruit buds was unaffected. Yet the total crop was materially increased, the corrected treatment means showing a 70 per cent. increase over the control trees, equivalent to an extra 775 bushels per acre over the five years. This increase in crop, unmistakable even in the second season, cannot be attributed to any indirect effect of improved growth ; some more immediate effect of Epsom salt spraying must be sought.

Although the fruit size may have been increased to some extent, the effect of Epsom salt sprays on cropping was due very largely to an increase in the number of fruits. This is consistent with the findings of Blanchet (1957), who reported that an effect of magnesium deficiency in apples was to reduce the number of fruits before a marked reduction in fruit size occurred. Possibly in this trial an improved fruit set was associated with the prevention of a magnesium-deficient condition in the blossom clusters ; further, it was observed that the fruitlets on the control trees quickly abscissed from spurs where the scorching of the primary leaves was severe. Fudge (1939) found that the high demand for magnesium in the developing grapefruit was associated with a corresponding depletion in the surrounding leaves, and Moon *et al.*

(1952) have similarly reported a marked translocation of magnesium from the primary spur leaves to the developing apple fruit.

The poorer response from low volume applications of Epsom salt may have resulted from the lower quantities applied, or from less efficient application due to the use of a paint spray gun and the inability to see the deposit ; there was no evidence that the high concentration was harmful.

The observed effect of urea sprays in increasing the number of fruits in the first season may have been a direct one and therefore not relevant to the problem of magnesium deficiency, for urea applications have been frequently reported to increase fruit setting in apples (Blasberg, 1953). Certainly there was no consistent evidence of any effect of urea spraying on the scorch or on the magnesium content of the leaves, such as has been reported from the use of nitrogenous fertilizers (Hoblyn, 1941 ; Boynton and Compton, 1944 ; Cain, 1953a). If such effects are due to either of the mechanisms proposed by Boynton and Compton (1944), then foliar sprays of urea would not be expected to produce the same responses, but if the nitrogen effect is to be attributed either to a mobilizing effect on magnesium (Cain, 1953b) or to an increase in the cation exchange capacity of the roots (McLean *et al.*, 1956), then it is conceivable that urea sprays could affect the magnesium nutrition in the same way as the reported effects of nitrogenous fertilizers. Whether direct or indirect in its effect on the numbers of fruits, urea was less clearly effective in this respect after the first year, and indeed it improved leaf colour and significantly increased the nitrogen content of the leaves only in the first season. These responses to nitrogen application in 1954 may have been associated with a relatively poor nitrogen status of the control trees as a result of grassing down only two years previously.

The results obtained in this trial, considered in relation to the widespread occurrence of magnesium deficiency symptoms in apple orchards, emphasize the urgent need for field trials to assess the growth and cropping response to magnesium sprays of commercial type trees on various soils and showing symptoms in different degrees of severity.

SUMMARY.

Magnesium-deficient dwarf pyramid apple trees of the variety Edward VII on M.VII rootstock were used in an experiment to test the efficacy of Epsom salt and urea sprays for the control of this disorder.

In each of the five years, five post-blossom applications of 2 per cent. Epsom salt ($MgSO_4.7H_2O$) sprays effectively increased the leaf magnesium content, delayed the onset of leaf symptoms and markedly reduced their subsequent severity. Although little evidence was obtained of a growth response and the number of fruit buds was not increased, the cropping was considerably improved. A suggestion is made that the increased number of fruits was related to the control of early-season deficiency symptoms on fruiting spurs.

Low volume applications of concentrated Epsom salt sprays, tested on a limited scale, were found to be practicable but appeared to be less effective than the usual sprays.

Sprays of 0·5 per cent. urea, though they did not raise the leaf magnesium status or control the foliar deficiency symptoms, increased the cropping, possibly because of a direct nitrogen effect on fruit setting or of a magnesium mobilization rôle.

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MALUS PLATYCARPA AS AN APPLE VIRUS INDICATOR

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THE occurrence of virus infection in commercial apple varieties and rootstocks grown in this country is known to be far more widespread than is suggested by the comparative rarity of symptoms on leaves, fruits or stems (1, 2, 4, 5). Apples in general seem to have a greater tolerance of virus than do the stone fruits and can often carry heavy infection without exhibiting any specific external symptoms. The study of these latent virus infections is nevertheless important : not only may a virus which is latent in one variety or rootstock produce disease symptoms on another less tolerant variety with which it is united by grafting, but there is a distinct possibility that so-called latent infections may in fact adversely affect the growth and cropping of the tree, even although they do not produce the spectacular symptoms usually associated with virus diseases.

The detection of latent virus infections in fruit trees depends on the transmission of the virus by grafting to a sensitive indicator plant. The variety Lord Lambourne, which is sensitive to apple mosaic, chat fruit and rubbery wood viruses, is the only indicator which has so far been used extensively for indexing apple rootstock and scion varieties in the search for healthy propagating material (1).

The purpose of this note is to draw attention to the value of *Malus platycarpa* Rehd. as an additional indicator of those latent viruses in the apple which do not produce symptoms on Lord Lambourne. The value of this indicator was discovered as the result of a systematic survey of 19 species and varieties of *Malus* and *Pyrus*, the following 18 of which proved of no value for this purpose : *M. baccata*, *M. baccata microcarpa*, *M. coronaria*, *M. florentina*, *M. aldenhamensis*, *M. denticulata*, *M. sikkimensis*, *M. micromalus*, *M. toringoides*, *M. prunifolia*, *M. prunifolia macrocarpa*, *M. prunifolia Rinkii*, *M. Sieboldii arborescens*, *M. orthocarpa*, *M.* " Mammoth Crab ", *P. Calleryana*, *P. Lindleyi*, *P. amygdaliformis*.

The original material of *M. platycarpa* was obtained from a tree in the Royal Botanic Gardens, Kew. It has since been propagated by budding or grafting on to apple seedling rootstocks or on to seedling stocks of the apomictic *Malus sikkimensis* (Hook.) Koehne (3). For indexing work, the latter stocks are preferable to crab seedlings on account of their genetic uniformity. *M. platycarpa* forms a good union with *M. sikkimensis* and, when virus free, grows vigorously, attaining an average height of three to four feet in the first year of growth.

The indexing experiments described in this paper were carried out by a double budding technique. Seedlings of *M. sikkimensis* were budded with *M. platycarpa* about four inches above soil level. Two inches below this bud, on the same side of the stock, the inoculation bud was inserted. During the following season the *M. platycarpa* bud was allowed to grow but the inoculation bud was rubbed off as soon as the bud shield had united with the stock.

Symptom expression on M. platycarpa.

The following types of symptom have been observed on young trees of *M. platycarpa* inoculated with buds taken from commercial apple varieties and rootstocks :

(1) *Line pattern* (Fig. 1, A and C). Leaves on infected trees are smaller than normal and are often somewhat distorted and cupped in shape. They show an irregular diffuse chlorotic line pattern with a tendency to form small but distinct ring-spots. Severely infected leaves are often shed prematurely.

(2) *Dwarfing* (Fig. 1, D). Inocula from many sources cause a very pronounced dwarfing of *M. platycarpa* during the maiden year. Usually this dwarfing is associated with the occurrence of line pattern, but this is not invariably so. Some dwarfing has been seen, in the absence of definite leaf symptoms, in trees inoculated with buds from Crab C rootstocks and from certain pear varieties, and it seems likely that a distinct virus or virus complex is responsible for this reduction in vigour. Dwarfing is, however, always more pronounced when line pattern is present, and may be still further accentuated by rubbery wood virus.

(3) *Scaly bark* (Fig. 1, B). The bark of one-year-old shoots takes on a roughened scaly appearance, often accompanied by slight swelling. These symptoms may occur on the main stem but are often particularly prominent near the base of one-year-old lateral shoots. Frequently the shoot becomes completely girdled and dies and, where infection is severe, the whole tree may be killed.

The virus nature of this symptom is open to some doubt as a fungus, so far unidentified, appears to be associated with the bark lesions and has been isolated from them. It is not at present clear whether this is a secondary infection or whether the fungus itself is the primary cause of the scaly bark condition. No scaly bark symptoms have been seen on uninoculated control trees of *Malus platycarpa*, which suggests that a virus transmitted from apple is the primary cause of the disorder. Alternatively it may be that the fungus is the primary agent but is only able to attack trees already weakened by infection with line pattern or other viruses.

Distribution of viruses.

Evidence has been obtained that the viruses responsible for inducing line pattern and dwarfing (and possibly scaly bark) in *M. platycarpa* are widely distributed in latent form in commercial apple varieties and clonal rootstocks. The results of a preliminary survey of 13 stocks and 17 scion varieties are given in Table I. The stocks indexed came from the Long Ashton stoolbeds, two buds being taken from each of two stools chosen at random. For the scion varieties a single bud was taken from each of two trees growing in the Long Ashton plantations. Budding and inoculation were carried out in 1956 and records of symptoms were made during June and October in 1957 and 1958. The height and diameter of the maiden trees were measured in the winter 1957/58, and the diameter of the two-year-old trees during October 1958.

Of a total of 79 inoculation buds used in this experiment 48 (61 per cent.) proved to be carrying latent line pattern virus. Twenty-two of the inoculated trees (28 per cent.) developed symptoms of scaly bark. Nearly all the trees which died did so during the second year after having exhibited severe symptoms of scaly bark during the first year, and it seems likely that the scaly bark was the direct cause of death.

The number of buds involved in this experiment is too small to enable firm

Table I.

Influence of inoculation buds from various rootstocks and scion varieties on the growth of Malus platycarpa *worked on* M. sikkimensis *seedling rootstocks.*

Source of inoculation bud	No. of trees inoculated	No. of trees showing :			No. of trees dead after 2 years	Mean height of maiden trees (cm.)	Mean diam. maiden trees (mm.)	Mean diam. 2-year trees (mm.)
		Line pattern	Scaly bark	No symptoms				
M.I	4	4	4	0	1	57	8	10
M.II	3	2	2	1	1	94	9	18
M.IV	3	2	2	0	1	79	8	12
M.VII	4	4	4	0	0	47	7	8
M.IX	4	4	2	0	2	38	5	6
M.XII	4	0	1	3	0	98	8	16
M.XVI	4	0	1	3	0	113	10	18
M.XXV	4	4	0	0	0	71	8	13
Crab C	4	0	0	4	0	81	7	11
MM.104	4	0	0	4	0	101	10	19
MM.106	4	0	0	4	0	109	10	19
MM.109	2	0	0	2	0	101	7	17
MM.111	3	0	0	3	0	96	8	13
Laxton's Superb ..	2	2	0	0	0	28	6	5
Emneth Early ..	2	2	1	0	1	91	8	9
Allington Pippin ..	2	2	0	0	1	69	8	8
Court Pendu Plat ..	2	2	1	0	0	68	9	13
Cox's Orange Pippin	1	1	1	0	0	68	7	8
Miller's Seedling ..	2	2	0	0	0	85	8	12
Cheddar Cross ..	2	2	0	0	0	75	6	9
Exeter Cross ..	2	2	0	0	0	62	9	17
Early Worcester ..	2	2	0	0	0	84	7	10
Late Orange ..	2	2	0	0	2	53	5	—
Merton Prolific ..	1	0	0	1	0	110	9	14
Ribston Pippin ..	2	2	2	0	0	63	6	10
Sturmer Pippin ..	2	2	0	0	0	54	4	5
Merton Worcester	2	0	0	2	0	93	9	13
Bramley's Seedling	2	1	0	0	2	54	—	—
Worcester Pearmain	2	2	1	0	1	75	6	6
Egremont Russet ..	2	2	0	0	0	64	8	11
Total	79	48	22	27	12	—	—	—
Controls	8	0	0	8	0	102	10	19

conclusions to be drawn concerning the degree of infection of different rootstock clones and scion varieties. It is of interest to note, however, that no infection was found in any of the four Malling-Merton stocks which were tested, whereas most of the older series of Malling stocks were carrying line pattern. Latent line pattern was also found in all four buds of the relatively new M.XXV stock. It will also be noted from Table I that inoculation buds from M.IX, M.I, M.VII and M.IV—all stocks in the less vigorous range—drastically reduced the vigour of *M. platycarpa*. Of the 17 scion varieties examined, all induced symptoms in *M. platycarpa* with the exception of Merton Prolific and Merton Worcester, both of which are relatively young varieties. There was also very pronounced dwarfing of the inoculated trees as compared with uninoculated controls. It must be emphasized that, although these viruses are

Plate I.

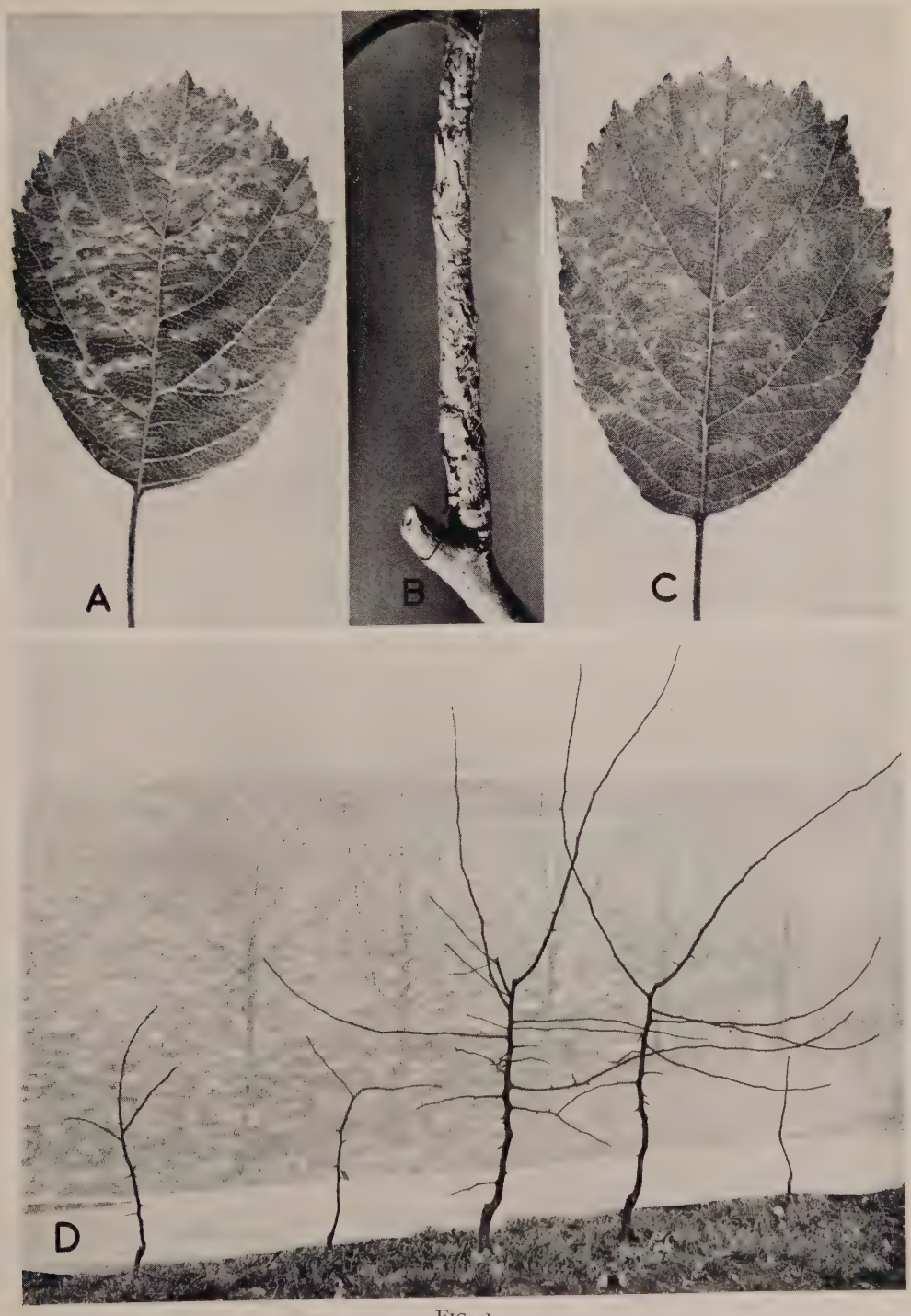

Fig. 1.

A, C : Line pattern symptoms on leaves of *Malus platycarpa*.
B : Scaly bark condition of *Malus platycarpa* following infection from M.VII rootstock.
D : *Left*, two 2-year-old trees of *Malus platycarpa* showing dwarfing resulting from infection from M.IX rootstock ; *right*, two 2-year-old control trees of *Malus platycarpa*.

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undoubtedly widely distributed in commercial apple varieties and rootstocks in this country, there is at present no evidence that they are in any way harmful, except to *Malus platycarpa*.

No symptoms have ever been induced on *M. platycarpa* as a result of budding or grafting on apple seedling rootstocks, suggesting that the viruses involved are not seed transmissible.

Reaction of Malus platycarpa *to known viruses.*

The virus responsible for line pattern symptoms on *M. platycarpa* is distinct from those causing rubbery wood, chat fruit and mosaic in Lord Lambourne. This was shown by inoculating *M. platycarpa* with buds from Lord Lambourne containing the respective viruses and also with buds from apparently healthy trees. Inocula from these four sources all induced dwarfing and caused line pattern on *M. platycarpa*, and the only additional symptoms seen were a few small white flecks on some leaves of the trees inoculated with a severe strain of apple mosaic.

Whilst line pattern is certainly not caused by the rubbery wood, the chat fruit or the apple mosaic virus, its possible relationship with other virus diseases of apple has not yet been investigated. Posnette and Cropley (6) have described line pattern symptoms which they observed in the apple variety Laxton's Superb and subsequently transmitted by grafting to various Malling-Merton rootstocks and to M.XXV. The visual symptoms on apple are similar to those of the line pattern on *M. platycarpa* described in this paper. The fact that *platycarpa* line pattern is symptomless on M.XXV and on Laxton's Superb, however, makes it doubtful whether the same virus is involved, though it is possible that the line pattern described by Posnette and Cropley is simply a more virulent strain of the *platycarpa* line pattern virus.

SUMMARY.

(1) Attention is drawn to the value of *Malus platycarpa* Rehd. as an indicator plant for certain apple viruses.*

(2) The following types of symptom have been observed on *M. platycarpa* inoculated with buds from apple : (*a*) line pattern on the leaves ; (*b*) dwarfing ; (*c*) a scaly bark condition which is associated with fungal infection.

(3) The viruses responsible for line pattern and dwarfing in *M. platycarpa* appear to be widely distributed in latent form in commercial apple varieties, and in the Malling series of clonal rootstocks. As far as is known, they produce no harmful effects. No infection was found in the four Malling-Merton rootstocks tested.

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* It is obviously desirable that other research workers in this field who wish to employ *M. platycarpa* as a virus indicator should use material from the same clone as was used in these experiments. Limited supplies of budwood of this clone can be obtained on application to Long Ashton Research Station.

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BOOK REVIEWS

NUTRITION OF THE LEGUMES. Edited by Professor E. G. HALLSWORTH. Proc. of the University of Nottingham 5th Easter School in Agricultural Science, 1958. (London: Butterworths Scientific Publications. 1958. Price 55s. Postage 2s.)

The supply of available nitrogen is often a limiting factor in plant growth in many parts of the world. The legumes, which are able to obtain their nitrogen requirements from the air through symbiosis with nitrogen-fixing bacteria, are the only important group of crop plants capable of producing satisfactory yields independently of supplies of combined nitrogen in the soil. The importance of an understanding of this symbiotic fixation of atmospheric nitrogen is therefore obvious.

This book serves not only to present some of the advances made in the knowledge of legume nutrition during recent years but also to emphasize the range of disciplines which are involved in any comprehensive study of the soil-bacteria-plant system. It is divided into five broad sections dealing with the plant component, the rhizobial component, the symbiotic system, the biochemical and the field aspects. It would be invidious to attempt to assess the relative merits of the individual contributions, since each chapter contains much valuable and often new information. Perhaps the most commendable feature of the book is that, although each section deals with a specific and often highly specialized aspect of legume nutrition, the interrelated nature of the various sections is maintained.

The great diversity of the legumes and their wide geographical distribution is outlined. Most of the crop and forage legumes of temperate regions belong to the Trifolieae and the Vicieae which represent only about 8 per cent. of the total species of the Leguminosae. These two tribes are adapted to highly fertile neutral or near-neutral soils while the bulk of the remaining leguminous species grow satisfactorily on acid soils of low nutrient status. These broad differences in nutritional requirements between the various species of legumes have often been overlooked in the past, and the attention given to them in the book is timely.

It has been possible for many years to correct many minor element deficiency conditions in the field by the application of sprays containing the appropriate nutrients, but in the legumes it has been a problem to decide whether the effect has been on the plant or on its associated nodule bacteria. Progress towards the elucidation of the minor nutrient requirements of both host and bacteria is reported, and the precise rôle of certain minor elements on the fixation of nitrogen by the legume-bacteria symbiosis is discussed.

An important advance in recent years in this field of plant nutrition has been the realization that not all strains of Rhizobium which infect a given host plant are of equal efficiency in fixing nitrogen and that the host range of a given strain of Rhizobium is limited. Inoculation of legume seeds with cultures of Rhizobium is widely used to assist in crop establishment in new areas, but present techniques are not always successful. The chapters devoted to this involved problem suggest that, until the fundamental principles underlying host specificity, physiology of infection

and effectiveness of the resulting symbiosis are more clearly understood, full exploitation of the agricultural potentialities of the nodulated legumes will not be possible.

The organizers of the conference are to be commended for having provided the opportunity for discussions between workers on the many aspects of the problem. Their judicious choice of order of presentation of the papers has resulted in a well-balanced book which, on account of the highly specialized nature of many of its chapters, is likely to be of more value to the specialist than to the general horticultural reader. F.H.

THE SCIENTIFIC PRINCIPLES OF CROP PROTECTION. By HUBERT MARTIN. (London : Edward Arnold (Publishers) Ltd., 1959. Pp. 359. Price 65s.)

All persons concerned with pest, disease and weed control will extend a great welcome to the fourth edition of Hubert Martin's book. Its publication is a notable event. Since 1928, when the first edition appeared, the book has been a constant and invaluable source of information on the materials and principles used in crop protection. Successive editions have fully maintained the high merit of the first ; this edition sets a new standard of excellence.

The title has been changed, " Plant Protection " giving way to " Crop Protection ", the term now generally accepted. The format closely follows that of the third edition. Chapters dealing with plant resistance to invading organisms, the influence of environmental factors on the liability of plants to attack and on biological control, are followed by discussions of spray formulations and adjuvants, fungicides, insecticides, acaricides, nematicides, weedkillers, fumigants, seed and soil treatments, traps and the treatment of centres and vectors of infection. The formidable task of bringing the book up to date without unduly increasing its size has been accomplished with great skill. Throughout there is evidence of careful editing and re-writing. The earlier work has been sifted and the new information happily blended with the old. The many new groups of synthetic compounds that have become available for crop protection purposes during the last decades are well described, and subjects that also receive attention include the fungicidal antibiotics, the virus diseases of insects, molecular structure and toxicity relationships, the principles of bioassay and hypotheses on the mechanics of toxic action.

The author succeeds admirably in his task of presenting to the entomologist and mycologist a detailed survey of the chemical and physico-chemical aspects of crop protection and of providing the chemist and physicist with a means of approach to the biological side. The book will be of the greatest value to both groups of workers.

It is attractively produced, lists of references are inset less frequently, thus making for better continuity of reading, and typing errors are remarkably few. The book presents an excellent account of the principles underlying crop protection which, as the author rightly points out, is no less fundamental to crop production than are cultivation and nutrition. J.T.M.

PUBLICATIONS RECEIVED.

ABSTRACTS AND INDEX TO THE ANNUAL RESEARCH REPORTS 1913–1953 EAST MALLING RESEARCH STATION. 1957. Pp. 175. Obtainable from the Secretary, price 20s. (Members 12s. 6d.)

The aim is not merely to index the Reports that have appeared during the first

forty years of the Station's existence but also by means of brief abstracts of each paper to summarize the development of research. Lists of pests and diseases mentioned in the Reports are included as appendices.

COMMON NAMES OF BRITISH INSECT AND OTHER PESTS. Ministry of Agriculture, Fisheries and Food, Technical Bulletin No. 6. (London : H.M. Stationery Office. 1957. Pp. 49. Price 7s. 6d.)

This bulletin follows the approved lists published by the Association of Applied Biologists in 1947 and 1952. It carries the authority of the Ministry's Infestation Control Division and the Plant Pathology Laboratory, and will be of great value both to authors and to the editors of scientific and other journals dealing with insect pests.

THE A.B.C. OF SOILS, INCLUDING MANURING, COMPOSTS AND LAWNS. By W. E. Shewell-Cooper. (London : The English Universities Press Ltd. 1959. Pp. 150, illus. Price 8s. 6d.)

SOIL SURVEY OF GREAT BRITAIN. Rep. No. 10, 1957. (London : H.M.S.O. 1958. Price 5s.)

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